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A revision of the extant species of *Theodoxus* (Gastropoda, Neritidae) in Asia, with the description of three new species

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Abstract

Asia contains a high species diversity of the freshwater gastropod genus *Theodoxus*. Recent molecular and morphological reviews of this diversity have uncovered a number of yet undescribed species while suggesting the urgent revision of several others. Moreover, some of these studies have indicated a number of species previously not recorded for this continent. Despite the advancements, a taxonomic revision and an update on the distribution of *Theodoxus* spp. in Asia is still pending. Here, we construct the most robust phylogeny of *Theodoxus* up to now and review original descriptions, type material, recent taxonomic revisions, compendia, and species lists to provide a comprehensive checklist of all known extant Asian *Theodoxus* spp. Our checklist also provides descriptions for three recently discovered and yet undescribed species (*Theodoxus gurur* Sands & Glöer, **sp. nov.**, *Theodoxus wesselinghi* Sands & Glöer, **sp. nov.**, and *Theodoxus wilkei* Sands & Glöer, **sp. nov.**), as well as shows the need to synonymise several previously described morphospecies. The present revision recognizes 14 extant *Theodoxus* spp. for Asia. Some of these species are widespread, while others are endemic to just a single location. Based on the revised and new distribution data, we provide updates and new assessments of species conservation statuses.

Key Words

checklist, conservation, morphology, Palearctic, phylogenetics, taxonomy

Introduction

The genus *Theodoxus* Montfort, 1810 is a common component of the aquatic malacofauna of the Western Palearctic. It plays an important role in the ecology of freshwater ecosystems by managing the growth of certain algae and acting as a food source for other organisms (Kiss-József Rékási and Richnovszkyt 1995; Lappalainen et al. 2001; Råberg and Kautsky 2008; Peters and Traunspurger 2012). Species of *Theodoxus* can be used as indicators of environmental health (Alhejoj et al. 2017) and setting (Moissette et al. 2016), which is of particular usefulness to (palaeo)ecologists. Moreover, some species are known to act as hosts for a number of trematodes and ciliates, which is of broad interest to parasitologists (Raabe 1968; Abdel-Hafez and Ismail 1987). To date, the genus *Theodoxus* includes more than 35 described extant species across Europe, western Asia, and northern Africa (Welter-Schultes 2012; Encyclopedia of Life 2018; IUCN 2019; MolluscaBase 2019; Glöer 2019) where they are found in freshwater to mesohaline aquatic environments (Bănărescu 1991; Bandel 2001).

The majority of interspecific diversity in *Theodoxus* occurs within western Asia (Sands et al. 2019a). The effects of tectonic history and past climatic changes have driven both ecological and geographical speciation, as well as

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immigration to this region (Sands et al. 2019a). Previous studies have recognised many species of *Theodoxus* here (e.g. Roth 1987; Schütt and Şeşen 1992, 1989b; Degani et al. 1992; Yıldırım 1999; Bößneck 2011; Mansoorian and Samaee 2012; Amr et al. 2014; Al-Abbad et al. 2015; Handal et al. 2015; Odabaşı and Arslan 2015; Gürlek et al. 2019). However, freshwater and brackish habitats in these parts of Asia are under threat from a variety of anthropogenic and climatic impacts (e.g. Dudgeon et al. 2006; Abbaspour et al. 2009; Gleick 2014, Lattuada et al. 2019), which could put many of these and other aquatic species at risk of extinction.

Properly identifying species is an important task for conservationists in order to coordinate preservation efforts. In the case of *Theodoxus*, many occurrences of species have been based on early, purely morphologically based species descriptions (e.g. Martens 1874, 1879; Westerlund 1886; Kobelt 1899). Despite the morphological species concept been shown to be useful for some species of *Theodoxus*, early descriptions were based on relatively few morphological characters, focusing mainly on shell shape and periostracum colouration and patterning. These characters have been shown to exhibit considerable intraspecific variation (Glöer and Pešić 2015; Alba et al. 2016; Anistratenko et al. 2017), which may be closely linked to environmental parameters (Neumann 1959; Heller 1979; Rust 1997; Zettler 2007; Mienis and Rittner 2017). This variation makes reliable identification challenging and has caused debate on the validity of some *Theodoxus* spp., including some of the Asian species discussed herein (e.g. Schütt and Şeşen 1989b; Glöer and Pešić 2012; Anistratenko et al. 2017; Wesselingh et al. 2019).

Presently, the phylogenetic species concept through molecular approaches has proved to be a reliable tool in substantiating species diversity in *Theodoxus*. Three studies have presented broad-scale phylogenetic outlooks on the interspecific diversity within *Theodoxus* (Bunje and Lindberg 2007; Sands et al. 2019a, 2019b). These phylogenetic studies have greatly improved our understanding of the relationships among species and have supported the outcomes of some more recent and detailed morphological reviews (Alba et al. 2016; Anistratenko et al. 2017; Glöer 2018; Wesselingh et al. 2019). While they have highlighted the need for revision and have indicated new species (see Sands et al. 2019a), a taxonomic revision of *Theodoxus* is still pending.

In this paper, we aim to revise the taxonomy of Asian *Theodoxus* spp. creating a checklist based on which we discuss aspects relevant for conservation. To reach this major objective we 1) construct an extended phylogeny incorporating published phylogenetic data and additional molecular data from Asian material, and 2) review type material and past morphological studies. Through this revision we update the geographic distribution of *Theodoxus* spp. in Asia. Moreover, we provide descriptions of as yet undescribed species recently identified. We hope that this study will aid species identification in *Theodoxus* and thus benefit conservation efforts.

Methods

Study region

The study region of Asia comprises mainly of western Asian countries: Armenia, Azerbaijan, Georgia, Iran, Iraq, Israel, Jordan, Lebanon, Syria, Turkey, and parts of Kazakhstan, Turkmenistan, and Uzbekistan.

Phylogenetics and species delimitation

Previously published phylogenetic relationships among species of *Theodoxus* are spread between a number of different studies (e.g. Bunje and Lindberg 2007; Sands et al. 2019a, 2019b). These phylogenies still lack some commonly recognised morphospecies. To consolidate and expand upon recommendations from these studies, we constructed a new, robust and time-calibrated Bayesian phylogeny. We supplemented data from published studies available on GenBank (Bunje and Lindberg 2007; Fehér et al. 2012; Sands et al. 2019a, 2019b) with new data produced herein to incorporate as many morphospecies and Asian localities as possible to allow for sound taxonomic inferences and distribution assessments (Suppl material 1: Table S1). Moreover, Sands et al. (2019a) identified three new species, which we describe herein. Their identifications were originally based on a limited number of samples, and their soft bodies were destroyed for molecular analyses in that study. Our phylogeny facilitates to confirm that new, fresh material from the same localities belongs to the same molecular operational taxonomic units identified by Sands et al. (2019a) (Suppl. material 1: Table S1).

Sampling, amplification, sequencing and the alignment of gene fragments largely followed the published methods of Sands et al. (2019a). In brief, fresh samples were either hand collected in shallow waters or dredged from boats in deeper waters. Using the same DNA extraction methods, primers and PCR cyclic conditions, two partial mtDNA fragments (cytochrome c oxidase subunit I (COI) and the 16S rRNA (16S)) and one partial nDNA fragment (ATP synthetase subunit alpha (ATPα)) were amplified, allowing for comparability with available GenBank sequences. LGC Ltd (Berlin, Germany) carried out purification and bidirectional Sanger sequencing. Sequences were trimmed and aligned in Geneious 10.1.2 (Biomatters Ltd 2017) using the Geneious alignment algorithm. In total, sequences from 528 specimens (460 from GenBank; 68 generated for the current study) were used. These represented six outgroup *Neritina* spp. and 41 commonly recognised *Theodoxus* morphospecies. Of these *Theodoxus* morphospecies, 39 had previously been incorporated in phylogenetic assessments and 21 of them had already been earmarked as probable taxonomic synonyms (Bunje and Lindberg 2007; Sands et al. 2019a, 2019b). The molecular dataset lacked sequences for *T. gloeri* Odabaşı & Arslan, 2015, for which fresh material could not be obtained.

The time-calibrated phylogeny was reconstructed using the phylogenetic software package BEAST 2.5.2 (Bouckaert et al. 2014). Input files were generated in BEAUti 2.5.2 (BEAST package) using a log-normal relaxed molecular clock approach with birth-death tree prior. Dating of selected nodes followed secondary dating using the 95% highest posterior density (HPD) intervals of nodal ages established by Sands et al. (2019a) and a normal distribution of the priors: the most recent common ancestor (MRCA) of all *Neritina* spp. (9.75 Mya; 95% HPD = 14.09–5.44 Mya) and the MRCA of all *Theodoxus* spp. (8.27 Mya; 95% HPD = 11.62–4.97 Mya). The program bModelTest 1.1.2 (Bouckaert and Drummond 2017) in BEAUti was selected to determine the best-fit model for each gene fragment alignment, which are simultaneously determined during runs (COI = variation TN93 with added r_{cg} and r_{ct} counts (121341); 16S = variation TN93 with added r_{gt} counts (121134); ATPα = HKY (121121)). MCMC simulations ran for 200,000,000 generations, sampling every 20,000 generations using BEAST 2.5.2 (BEAST package) and implemented through the CIPRES Science Gateway (Miller et al. 2010). For congruency, two independent runs were performed. Validation of convergence and mixing was assessed using Tracer 1.7.1 (Rambaut et al. 2018) to ensure that all effective sample size (ESS) values were >200 for each run. LogCombiner 2.5.2 (BEAST package) was used to combine log and tree files applying a 50% burn-in, and trees were summarized in TreeAnnotator 2.5.2 (BEAST package) with no further burn-in.

To delimit species of *Theodoxus*, Sands et al. (2019a) used a combination of uncorrected COI *p*-distances (barcoding) and phylogenetic support. Based on morphospecies that formed supported, monophyletic entities, they considered mean p-distances >2.50% interspecific diversity and <2.00% intraspecific diversity. When *p*-distances lay between these thresholds, they used the nearest supported node encompassing a monophyletic group to define the species. To delimit species in this study, we compared the phylogenetic relationship of all additional sequenced material to the sequence data (species) incorporated from Sands et al. (2019a, 2019b).

Species distribution

Occurrence maps of *Theodoxus* spp. in Asia were constructed in the open source software QGIS 3.8.2 (https://www.qgis.org) using GPS coordinate data from the specimens incorporated into our molecular analyses. For *T. gloeri*, which lacks molecular data, we added only occurrences that we considered reliable, i.e. the type and paratype localities.

Photographing and morphological descriptions

Photographs of shells and opercula were made with a Keyence VHX-2000E digital microscope in conjunction with the program VHX-2000 Communication software version 2.3.5.0 (Keyence Corporation 2009–2012). Specimens photographed either represent individuals directly used in the dated phylogeny or formed part of the same collection (same date and location of collection) and conform morphologically (Suppl. material 1: Table S2). To provide a thorough overview of the species' phenotypic plasticity, also specimens from outside the study region are shown. Additionally, we used photographs of type material supplied by various collections (Suppl. material 1: Table S2). For the species newly described herein, the radulae were photographed with a field-emission scanning electron microscope DSM982 Gemini (Carl Zeiss GmbH, Germany) at the Justus Liebig University Giessen, Imaging facility.

We describe the shell shape, periostracum colouration and patterning, operculum features, and radula characters for each of the new species (Fig. 1). In the morphological

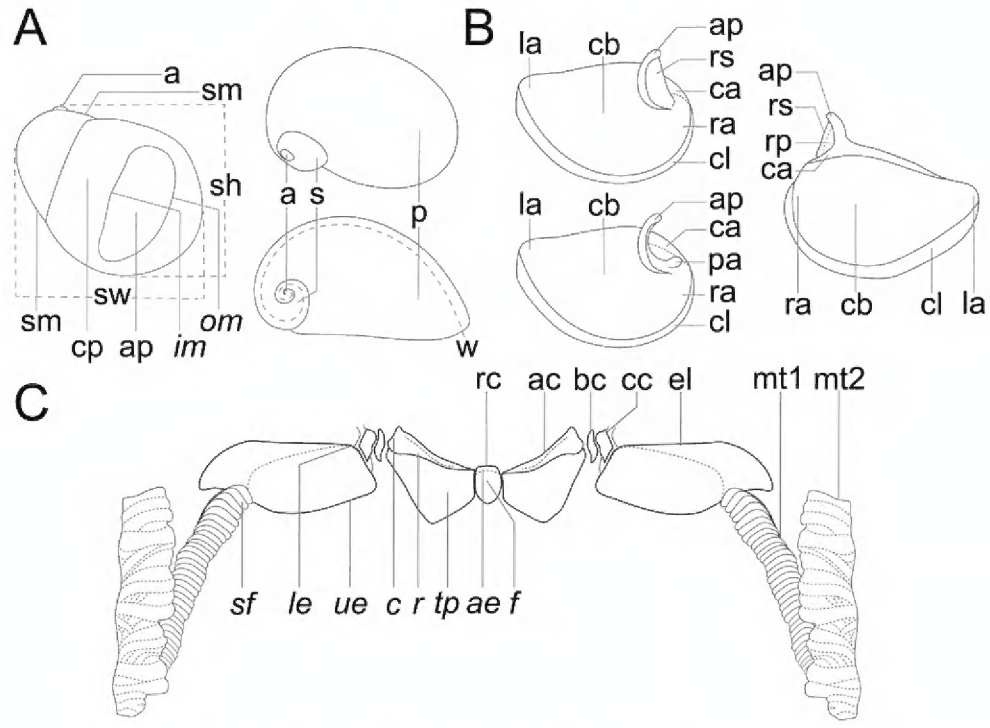

Figure 1. Terminology of key morphological characters for *Theodoxus*. **A**. Shell: a = apex, ap = aperture (*im* = inner margin, *om* = outer margin), cp = columellar plate, p = periostracum, s = spire, sh = shell height, sm = shell margin, sw = shell width, w = whorls; **B**. Operculum: ap = apophysis, ca = callus, cb = calcareous base, cl = conchioline lamella, la = left adductor, pa = pseudo-apophysis, ra = right adductor, rp = rib-pouch, rs = rib-shield; **C**. Radula: ac = A-central (*c* = cusp, *r* = ridge, *tp* = tooth plate), bc = B-central, cc = C-central, el = E-lateral (*le* = lower edge, *ue* = upper edge), mt1 = first row of marginal teeth (*sf* = small face of marginal teeth), mt2 = second row of marginal teeth, rc = R-central (*ae* = anterior edge, *f* = tooth face).

descriptions and comparisons, special emphasis is given to the operculum, which has been suggested to contain morphological characters particularly useful for species distinction (Glöer and Pešić 2015; Alba et al. 2016; Anistratenko et al. 2017). Here, we pay specific attention to the attenuation of the apophysis, the presence or absence of a pseudo-apophysis, the presence or absence of a rib-shield and rib-pouch (and the size thereof), and the strength of the callus on the calcareous base of the operculum (Fig. 1). Radulae were extracted and processed following Delicado et al. (2016), and the terminology of their morphological characteristics is based on Baker (1923) (Fig. 1).

Results

Taxonomic relationships and molecular conformity

Unsurprisingly the dated phylogeny closely resembles those presented by Sands et al. (2019a, 2019b) both in the dates established and the relationship between interspecific entities (Fig. 2; Suppl. material 1: Table S3). As no conflict among interspecific relationships occurred between these phylogenies, our phylogeny provides a valuable extension of the pre-existing phylogenetic framework.

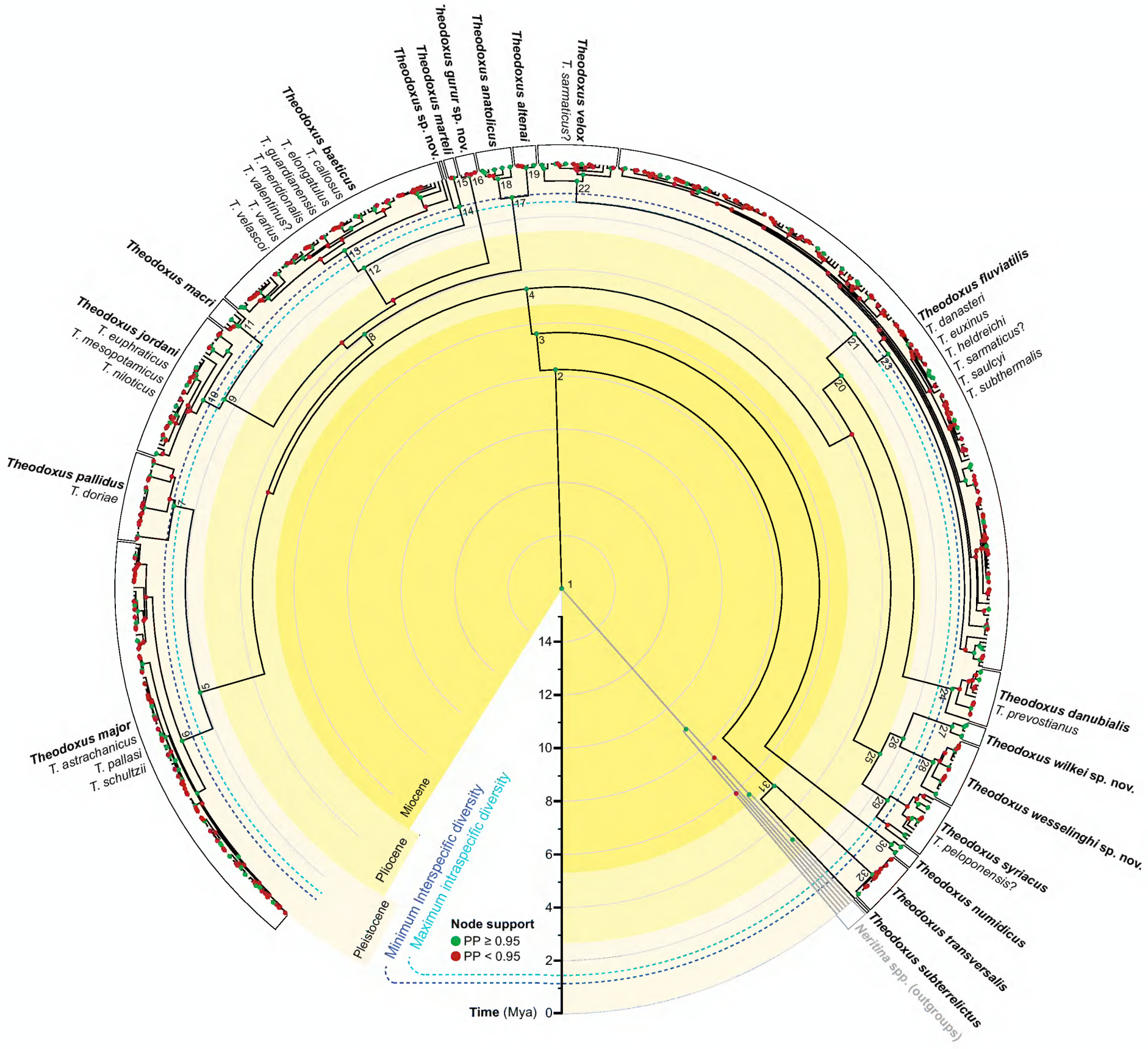

Figure 2. Dated phylogeny of the genus *Theodoxus* constructed with BEAST, based on existing GenBank and newly incorporated data for COI, 16S and ATPα (Suppl. material 1: Table S1). Morphospecies where associations are queried are highlighted by a question mark after the species name (see the "Systematic checklist" for more information). Small green (PP ≥ 0.95) and red (PP < 0.95) dots on nodes indicate the relative posterior probability support of divergence events. Node labels (1–32) correspond to divergence dates and HPD intervals in millions of years ago (Mya) for selected nodes (see Suppl. material 1: Table S3). Dashed dark blue and light blue lines represent the minimum interspecific and maximum intraspecific variation determined by Sands et al. (2019a) to aid *Theodoxus* spp. delimitation (see see Methods, Phylogenetics and species delimitation and that study for more information on the delimitation methods).

Of the new sequences incorporated herein, all specimens fell within the boundaries of pre-established species with no additional interspecific lineages emerging (see Methods, Phylogenetics and species delimitation; Sands et al. 2019a, 2019b; Fig. 2). Moreover, sequences from fresh material collected at the sites that harboured the novel lineages identified by Sands et al. (2019a) were concordant with the published sequences from that study (Fig. 2). In total, 19 species of *Theodoxus* were identified with 13 present in Asia. Our results confirmed findings of previous studies that many recognized morphospecies do not represent distinct phylogenetic species (Bunje and Lindberg 2007, Sands et al. 2019a, 2019b; Fig. 2). Additionally, our phylogeny included material of *T. euphraticus* (Mousson, 1874) and *T. mesopotamicus* (Mousson, 1874), which have never been phylogenetically assessed before and are found to be identical with *T. jordani* (G.B. Sowerby I, 1836) (Fig. 2).

Systematic checklist and new species descriptions

In the following checklist, we incorporate information from original descriptions, taxonomic revisions, compendia providing illustrations (e.g. Martens 1874, Kobelt 1899), as well as species lists and selected records that are relevant for the study area or require further discussion, and compare these to the latest phylogenetic results (also see Fig. 2). Based on these data, we discuss the identities, taxonomic relationships, geographic distributions (Fig. 3) and nomenclatural issues related to Asian species of *Theodoxus*. Whereabouts of type materials are provided as far as known. We examined 697 specimens in total (Suppl. material 1: Tables S1, S2), including the new material (incorporated for the first time herein), type specimens, and the material analysed by Sands et al. (2019a, 2019b). All species are illustrated, with focus on available type material and variation of conchological features and colour patterns. The supra-generic systematics follow Bouchet et al. (2017).

Institutional abbreviations used are:

BMNH Natural History Museum London, United Kingdom;
BMSM Bailey-Matthews National Shell Museum, Sanibel, Florida, United States of America;
COMULM Çanakkale Onsekiz Mart University, Limnology Museum, Çanakkale, Turkey;
OGUHB Eskişehir Osmangazi University, Museum of Hydrobiology, Eskişehir, Turkey;
IZAN I.I. Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine, Kiev, Ukraine;
LSL The Linnean Society of London, Division of Invertebrates I, London, United Kingdom;
MHNG Muséum d'histoire naturelle, Genève, Switzerland;

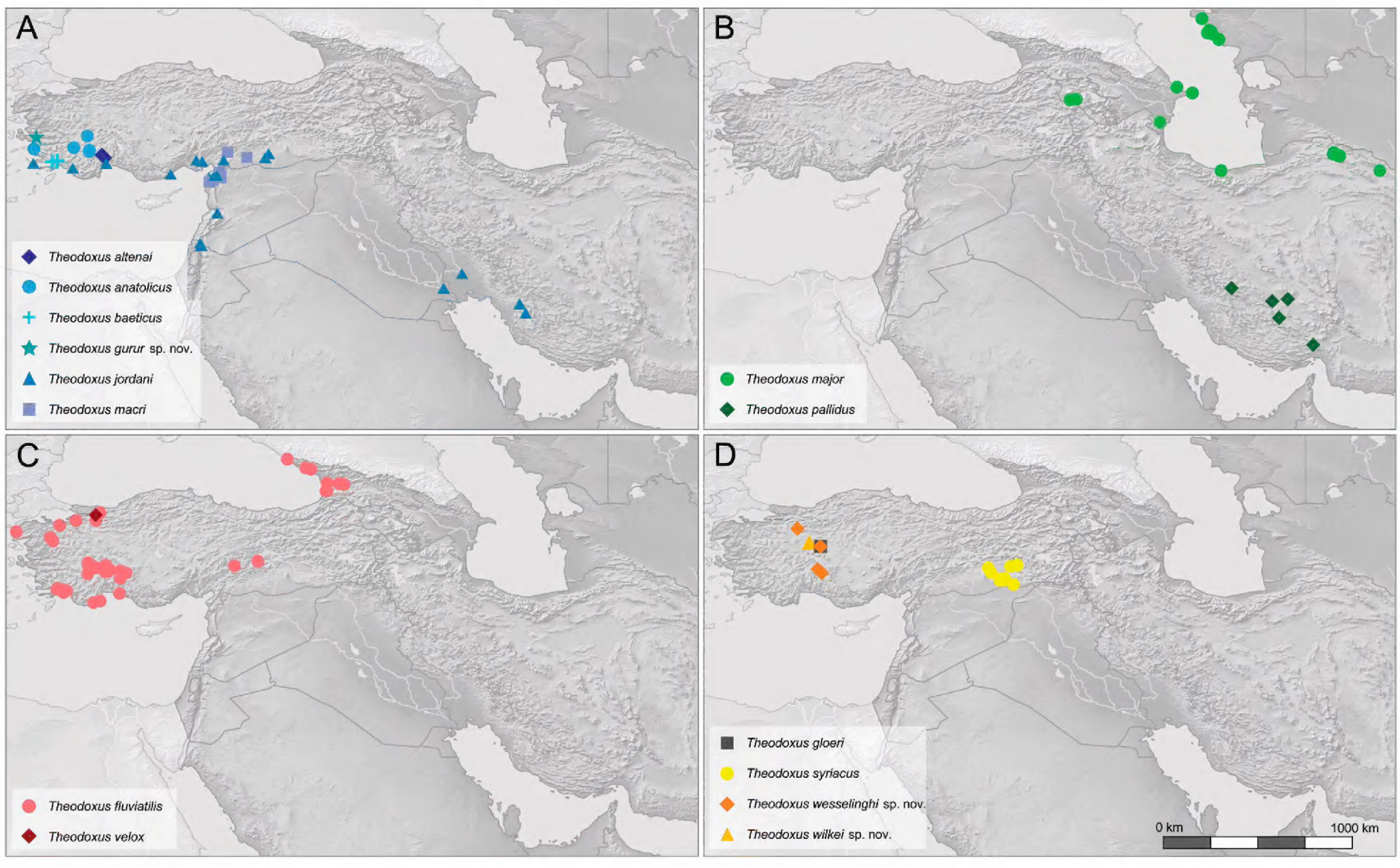

Figure 3. Occurrence map for *Theodoxus* spp. in Asia. All points conform to specimens used in the phylogenetic analyses (Suppl. material 1: Table S1), except for *T. gloeri* for which no molecular data are available and only the type and paratype localities are indicated. Species are partitioned across four identical maps (**A–D**) to limit overlap of points as far as possible. Barring *T. gloeri*, closer related species are grouped together (Fig. 2).

MNHN Muséum national d'Histoire naturelle Paris, France;
MRSN Museo Regionale di Scienze Naturali, Torino, Italy;
MSNG Museo Civico di Storia Naturale "Giacomo Doria", Genova, Italy;
NMNL Naturalis Biodiversity Center Leiden (formerly Rijksmuseum van Natuurlijke Historie), The Netherlands;
NMW National Museum of Wales, Cardiff, United Kingdom;
NSMF Senckenberg Research Institute and Natural Museum, Frankfurt am Main, Germany;
RBINS Royal Belgian Institute of Natural Sciences, Brussels, Belgium;
UGSB Justus Liebig University Giessen, Systematics and Biodiversity collection, Germany;
UCBL Université Claude Bernard Lyon 1, Villeurbanne, France;
ZIN Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia;
ZMB Museum für Naturkunde in Berlin, Germany;
ZMD B. Dybowski Zoological Museum of Lviv University, Lviv, Ukraine;
ZMH Zoological Museum, Hamburg, Germany;
ZMZ Zoological Museum Zurich, Switzerland;
ZSM Zoologische Staatssammlung München, Germany.

Class Gastropoda Cuvier, 1795
Subclass Neritimorpha Golikov & Starobogatov, 1975
Order Cycloneritida Frýda, 1998
Superfamily Neritoidea Rafinesque, 1815
Family Neritidae Rafinesque, 1815
Subfamily Neritininae Poey, 1852

Genus *Theodoxus* Montfort, 1810

Type species. *Theodoxus lutetianus* Montfort, 1810 [= *T. fluviatilis* (Linnaeus 1758)]; by original designation. Recent; Western Palearctic.

Theodoxus altenai Schütt, 1965

Figure 4A–G

Theodoxus (*Theodoxus*) *altenai* Schütt 1965: 46–49, pl. 1, fig. 4; Schütt and Şeşen 1992: 66; Yıldırım 1999: 885.

Theodoxus altenai: Roth 1987: 75; Kebapçı and Yıldırım 2010: 77; Gürlek et al. 2019: 2993; Glöer 2019: 37, fig. 19.

Type locality. Lake Kırkgöz, Kırkgöz Kaynağı spring complex, Döşemealtı, Antalya, Turkey.

Type material. Holotype (RNL V.56/1) and paratypes (RNL V.56) are stored in NMNL. Additional paratypes are stored in ZSM (ZSM/Mol – 20013211.00).

Remarks. The phylogenetic results based on mtDNA and nDNA (Fig. 2) suggest *T. altenai* Schütt, 1965 shares a close sister relationship with *T. anatolicus* (Récluz, 1841),

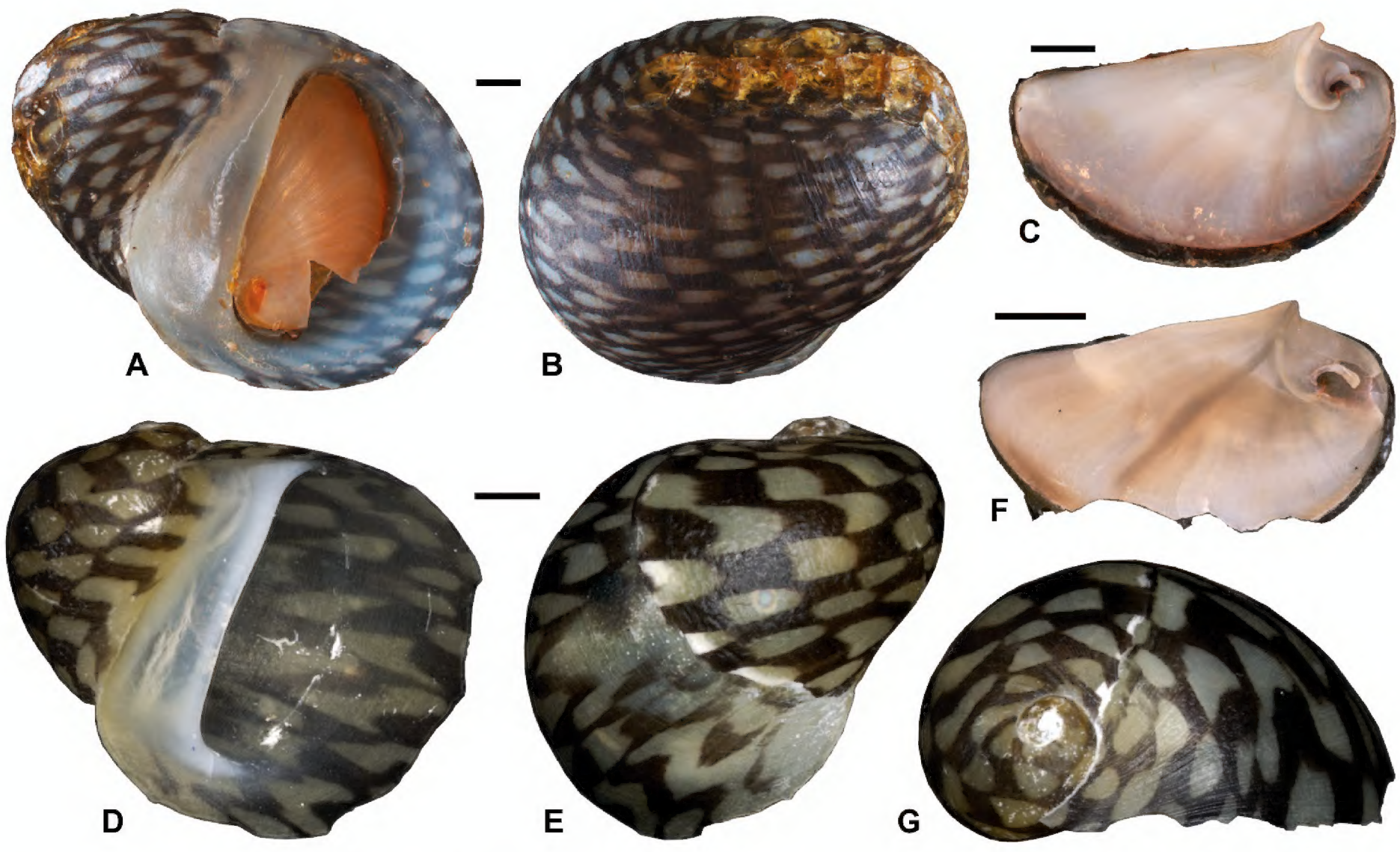

Figure 4. *Theodoxus altenai* Schütt, 1965. **A–C**. Holotype from Lake Kırkgöz, Döşemealtı, Antalya, Turkey (RNL V.56/1, NMNL). **D–G**. Topotype (UGSB 24167) incorporated into the phylogeny (Fig. 2). Scale bars: 1 mm.

where the two species likely diverged in the early Pleistocene (Sands et al. 2019a; Fig. 2). The pseudo-apophysis on the operculum of *T. altenai* is strongly curved and depressed and lies in the plane of the right adductor, while in *T. anatolicus* the pseudo-apophysis is more diagonal and less depressed (Figs 4, 5). Schütt (1965) wrote in his original description of *T. altenai* that there is no pseudo-apophysis but a short strongly curved depressed lamella instead. Furthermore, the periostracum colouration of *T. altenai* and *T. anatolicus* can be differentiated by brown and ivory checks as opposed to being uniformly black in the latter (Figs 4, 5). Moreover, the columellar plate extends beyond the shell margin in *T. altenai* (Figs 4, 5).

Distribution. All reliable records of this species were attributed to the Kırkgöz Kaynağı spring complex around Döşemealtı, Antalya, Turkey (Schütt 1965; Geldiay and Bilgin 1969; Bilgin 1980; Yıldırım 1999; Kebapçı and Yıldırım 2010; Gürlek et al. 2019; Fig. 3A). However, Sands et al. (2019a) indicated the species is also present at the Düden Waterfall, Varsak Karşıyaka, Antalya, Turkey (Fig. 3A).

Theodoxus anatolicus (Récluz, 1841)

Figure 5A–G

Nerita Anatolica Récluz 1841: 342–343, pl. 1, fig. 3 (partim, only regarding material from İzmir).

Neritina belladonna Mousson 1874: 16.

Neritina anatolica: Martens 1879: 86–88, pl. 3, figs 4, 5, pl. 13, figs 17–19, 25–29; Kobelt 1899: 3–4, pl. 211, figs 1321–1324.

Theodoxus (*Neritaea*) *anatolicus*: Bilgin 1980: 37–38; Schütt and Şeşen 1992: 65–66.

Theodoxus anatolicus: Yıldırım 1999: 885; Kebapçı and Yıldırım 2010: 77; Gürlek et al. 2019: 2993; Glöer 2019: 38, fig. 20.

Type locality. Smyrna (= İzmir), Turkey; Aleppo, Syria; Sidon, Lebanon; Scio (= Chios), Greece.

Type material. A set of nine syntypes of *N. anatolica* from İzmir is stored in MHNG (coll. no. MHNG-MOLL-15028), seven syntypes from Chios are stored in MNHN (coll. no. MNHN-IM-2000-32519) (also see Kabat and Finet 1992). The syntypes from İzmir and Chios differ considerably and might even represent different species. In order to bring stability to the taxonomy of this species, we designate one of the syntypes from İzmir (MHNG-MOLL-15028) as the lectotype (Fig. 5E–G). Twenty-three syntypes of *N. belladonna* from İskenderun ("Alexandretta"), Turkey, are stored in ZMZ (coll. no. 528908–528909).

Remarks. Schütt and Şeşen (1989b) indicated a close relationship among *Theodoxus* that contained a pseudo-apophysis on the operculum such as *T. anatolicus*, *T. cinctellus* (Martens, 1874) [= *T. jordani*], *T. euphraticus* [= *T. jordani*], and *T. jordani*, where they suggested these species could still be differentiated based on structural details of the operculum. Bunje and Lindberg (2007), using mtDNA, could not find a distinct *T. anatolicus* clade, and their specimens either grouped with *T. jordani* or *T. baeticus* (Lamarck, 1822). It is possible that the specimens used in that study may have been misidentified, as Sands et al. (2019a), using mtDNA and nDNA of material conforming to *T. anatolicus* from near İzmir, found an independent monophyletic clade. Their clade shares a close sister relationship with *T. altenai* and is distinct from both *T. jordani* and *T. baeticus* (Sands et al. 2019; also see Fig. 2). According to our analyses, the divergence of *T. altenai* and *T. anatolicus* likely occurred during the early Pleistocene (Sands et al. 2019a; Fig. 2). *Theodoxus anatolicus* and *T. altenai* also depict noticeable morphological differences. The periostracum patterning is more uniformly black in *T. anatolicus* as opposed to checkered ivory and brown in *T. altenai* (Figs 4, 5). Moreover, the columellar plate does not extend past the shell margin in *T. anatolicus* as it does in *T. altenai* (Figs 4, 5). *Neritina belladonna* was considered a synonym of *T. anatolicus* by Martens (1879), which we follow herein.

Distribution. Martens (1874) suggested *T. anatolicus* to have a very wide distribution range across Anatolia, Mesopotamia, and some of the Turkish and Greek Aegean islands. Roth (1987) revised this view and indicated *T. anatolicus* to be restricted to southern parts of western Anatolia and referred eastern Anatolian occurrences to *T. jordani*. Schütt and Şeşen (1989b, 1992) followed a more intermediate approach, suggesting that *T. anatolicus* occurred north-west of Hatay province in southern Turkey. Bank (2006) indicated the presence of this species on the Greek Aegean Islands, once again expanding the distribution range in support of Martens (1874); however, comprehensive sampling by Sands et al. (2019a) only found genetic evidence for *T. anatolicus* from south-western Anatolia, corroborating Roth (1987) (Fig. 3A).

Theodoxus baeticus (Lamarck, 1822)

Figures 6A–V, 7A–P, 8A–P

Neritina Baetica Lamarck 1822: 188; Martens 1879: 234–235, pl. 23, figs 1, 2; Kobelt 1899: 13–14, pl. 214, figs 1350, 1356.

Neritina varia: Menke 1828: 27 (nomen nudum).

Neritina callosa Deshayes in Geoffroy Saint-Hilaire et al. 1835: 156, pl. 19, figs 16–18; Martens 1879: 232–233, pl. 22, figs 27–30; Kobelt 1899: 11–12, pl. 213, figs 1345, 1346.

Neritina varia Rossmässler 1835: 18; Martens 1879: 225–226, pl. 21, figs 17–19; Kobelt 1899: 9, pl. 213, figs 1338.

Nerita meridionalis Philippi 1836: 159–160, pl. 9, fig. 13.

Nerita Philippii Récluz 1841: 341–342.

Neritina elongatula Morelet 1845: 96–97, pl. 9, fig. 4; Martens 1879: 228–229, pl. 22, figs 16–19; Kobelt 1899: 10–11, pl. 213, figs 1341, 1342.

Neritina inquinata Morelet 1845: 93–94, pl. 9, fig. 2.

Neritina guadianensis Morelet 1845: 95–96, pl. 9, fig. 3; Martens 1879: 231–232, pl. 22, figs 22–26; Kobelt 1899: 16, pl. 215, figs 1357, 1358.

Neritina violacea Morelet 1845: 92–93, pl. 9, fig. 1.

Neritina Velascoi Graells 1846: 20–21, unnumbered plate, figs 25–30.

Neritina Anatensis G.B. Sowerby II 1849: 535, pl. 116, figs 247, 248.

Neritina meridionalis: Martens 1879: 227–228, pl. 4, figs 27–29, pl. 22, figs 11–15; Kobelt 1899: 9–10, pl. 213, figs 1339, 1340.

Neritina Hidalgoi Crosse 1880: 320–322; Kobelt 1899: 12, pl. 214, fig. 1347.

Theodoxus (*Neritaea*) *varius callosus*: Bank 2006: 52.

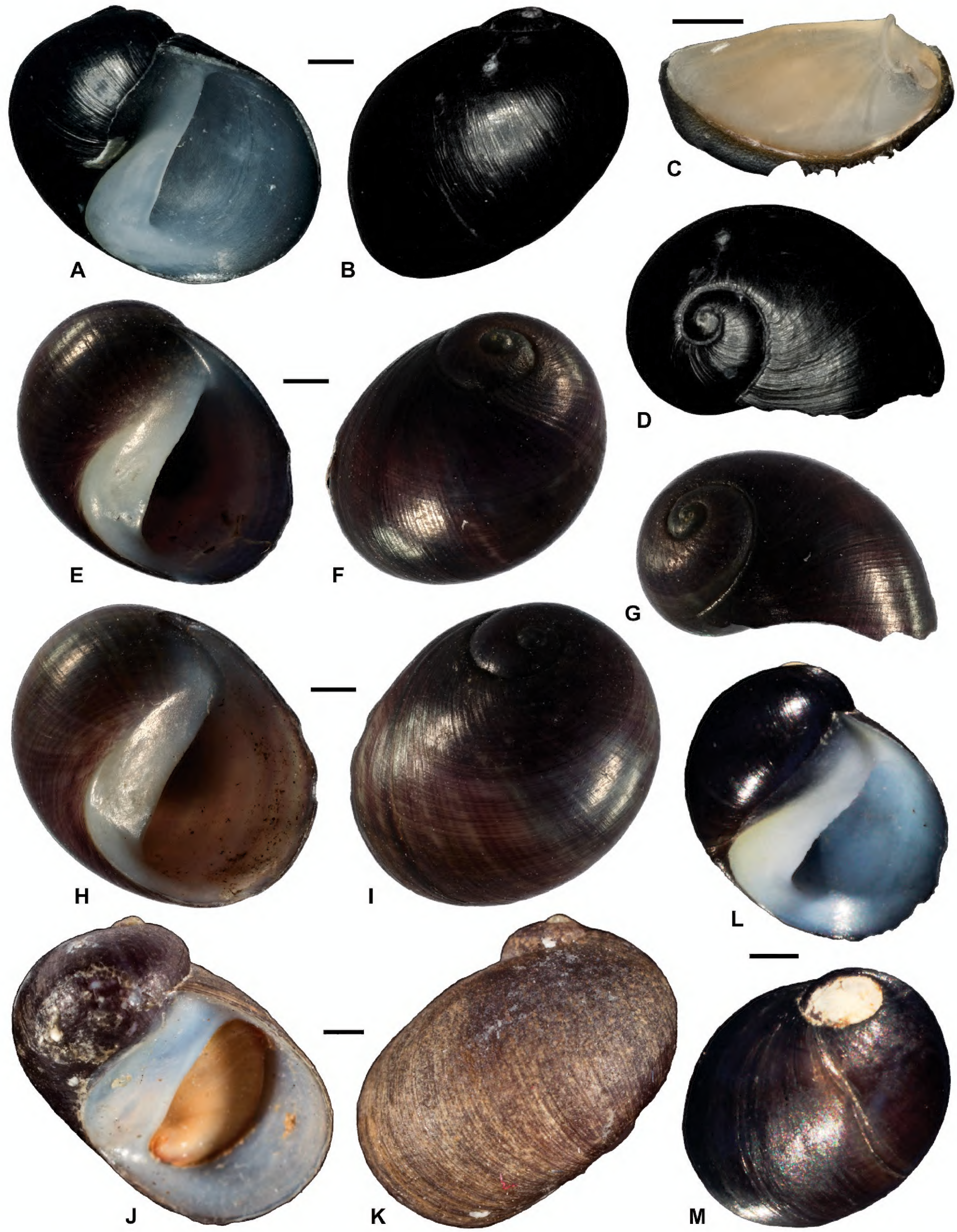

Figure 5. *Theodoxus anatolicus* (Récluz, 1841). **A–D**. Specimen collected at Işıklı, Denizli, Turkey (UGSB 24168) incorporated into the phylogeny (Fig. 2); **E–G**. Lectotype of *N. anatolica* from Izmir, Turkey (MHNG-MOLL-15028). **H**, **I**. Paralectotype of *N. anatolica* from Izmir, Turkey (MHNG-MOLL-15028); **J**, **K**. Paralectotype of *N. anatolica* from Chios, Greece (MNHN-IM-2000-32519); **L**, **M**. Syntype of *N. belladonna* from Izmir, Turkey (ZMZ 528908). Scale bars: 1 mm.

Theodoxus (*Neritaea*) *varius varius*: Bank 2006: 52.

Theodoxus baeticus: Glöer 2018: 135–136, figs 5–16; Glöer 2019: 38–39, figs 21, 22.

Theodoxus elongatulus: Welter-Schultes 2012: 27, unnumbered text figures.

Theodoxus meridionalis: Alba et al. 2016: 48, figs 4, 9; Glöer 2019: 46–47, fig. 33.

Theodoxus velascoi: Welter-Schultes 2012: 30, unnumbered text figures.

Theodoxus (*Theodoxus*) cf. *meridionalis*: Alba et al. 2016: 44–52, figs 2, 3, 5.

Theodoxus callosus: Glöer 2019: 39–40, fig. 23.

Type locality. Freshwaters of Andalusia, Spain (no precise locality given).

Type material. Two syntypes of *N. baetica* are stored in MHNG (coll. no. MHNG-MOLL-51319). We designate here the syntype illustrated in Figure 6E–G as lectotype (MHNG-MOLL-51319). Forty syntypes of *N. meridionalis*, consisting mainly of empty shells in addition to a few specimens with operculum, are housed in ZMB (without coll. no.; Glöer 2018). The holotype (by monotypy) of *N. callosa* is supposed to be stored in UCBL (coll. no. UCBL-EM 33336), but it could not be found (E. Robert pers. comm. 07/2018).

Remarks. Across the Mediterranean region a number of widely used nominal species exist that show considerable variation in shell shape and periostracum patterning, yet relatively similar operculum structures (including the presence of a pseudo-apophysis, ivory colouration of the calcareous base of the operculum, and a minimal rib-shield; Figs 6–8). These species include *T. baeticus*, *T. callosus* (Deshayes in Geoffroy Saint-Hilaire et al. 1835), *T. varius* (Rossmässler, 1835), *T. meridionalis* (Philippi, 1836), *T. elongatulus* (Morelet, 1845), *T. guadianensis* (Morelet, 1845), *T. velascoi* (Graells, 1846), and *T. valentinus* (Graells, 1846), as well as a number of species already synonymised under the above, including *Nerita philippii* Récluz, 1841, *Neritina inquinata* Morelet, 1845, *Neritina violacea* Morelet, 1845, *Neritina anatensis* G.B. Sowerby II, 1849, and *Neritina hidalgoi* Crosse, 1880. Most of these species were described from the Iberian Peninsula. Recent insights from molecular phylogenetics and morphological reviews indicate the presence of either a single species (*T. meridionalis*) or two species (*T. meridionalis* and *T. valentinus*), while all others may be considered junior synonyms (Bunje and Lindberg 2007; Ramos 2014; Martínez-Ortí et al. 2015; Alba et al. 2016; Sands et al. 2019a). Based on a reinvestigation of type material, Glöer (2018) recently showed that *T. meridionalis* is a junior synonym of *T. baeticus*. *Theodoxus baeticus* has previously been considered a junior synonym of *T. fluviatilis*, a view that was first rejected on the basis of molecular data by Bunje and Lindberg (2007). Here, we consider all species listed above except for *T. valentinus* as synonyms of *T. baeticus*. *Theodoxus valentinus* differs from *T. baeticus* in its unique shell shape, showing a high spire and two bulgy keels. Specimens with similar morphology obtained from near-by the type locality of *T. valentinus* (near Xàtiva, Spain) grouped with *T. baeticus* in our analyses (Figs 2, 8Q–T; Suppl. material 1: Table S1), which may suggest the two species are synonyms. We refrain here from a final conclusion on the matter until topotypic material of *T. valentinus* is genetically studied.

Our phylogenetic analysis indicate that *T. baeticus* diverged from other species likely during the early Pleistocene and shares a close relationship with an undescribed species from Spain (see Sands et al. 2019a) and *T. marteli* (Pallary, 1918) from northern Africa (Fig. 2).

Distribution. Considering the synonymies proposed here, *T. baeticus* is a widespread species throughout the Mediterranean region. It is present across the Iberian Peninsula, the Balearic Islands, Sicily, Tunisia, and the Balkans (Bănărescu 1991; Bandel 2001; Bank 2006; Fehér and Erőss 2009; Zettler and van Damme 2010; Martínez-Ortí et al. 2015; Sands et al. 2019a). Within our study region, the species is only noted from the freshwater drainages of the Gulf of Gökova in south-west Anatolia (Fig. 3A).

Theodoxus fluviatilis (Linnaeus, 1758)

Figures 9A–S, 10A–L

Nerita fluviatilis Linnaeus 1758: 777.

Theodoxus lutetianus Montfort 1810: 351–352.

Neritina Saulcyi Bourguignat 1852: 25–26.

Theodoxus fluviatilis var. *subthermalis* Issel 1865: 22–23; Issel 1866: 406–407.

Neritina fluviatilis: Martens 1879: 204–221, pl. 21, figs 1–6; Kobelt 1899: 16–18, pl. 215, figs 1359–1365.

Neritina Heldreichi Martens 1879: 225, pl. 22, figs 9, 10; Kobelt 1899: 9, pl. 213, fig. 1337.

Neritina euxina Clessin 1886: 55.

Neritina (*Theodoxus*) *heldreichi* var. *graeca* Westerlund 1886: 152.

Neritina brauneri Lindholm 1908: 217.

Neritina danubialis var. *Danasteri* Lindholm 1908: 215–217.

Neritina fluviatilis var. *abrauensis* Milaschewitsch 1914: 429–430.

Theodoxia Ghigii Gambetta 1929: 107, fig. 23.

Theodoxus dniestroviensis Put' 1972: 80–82, text fig. 5.

Theodoxus (*Theodoxus*) *heldreichi fluvicola* Schütt and Şeşen 1992: 64–66.

Theodoxus fluviatilis euxinus: Yıldırım 1999: 885.

Theodoxus fluviatilis fluviatilis: Yıldırım 1999: 884.

Theodoxus heldreichi fluvicola: Yıldırım 1999: 885 (as "*fluviocola*"); Kebapçı and Yıldırım 2010: 77; Gürlek et al. 2019: 2993.

Theodoxus (*Theodoxus*) *heldreichi*: Yıldırım 1999: 885.

Theodoxus subthermalis: Yıldırım 1999: 885–886; Sitnikova et al. 2012: 88–89, fig. 1A–F.

Theodoxus (*Theodoxus*) *heldreichi heldreichi*: Yıldırım 2004: 99, pl. 1, fig. 1.

Theodoxus fluviatilis: Anistratenko 2005: 7–8, figs 3, 4; Gürlek et al. 2019: 2993; Glöer 2019: 41–43, figs 26, 27.

Theodoxus heldreichi heldreichi: Kebapçı and Yıldırım 2010: 77; Gürlek et al. 2019: 2993.

Theodoxus brauneri: Welter-Schultes 2012: 27.

Theodoxus euxinus: Welter-Schultes 2012: 27, unnumbered text figures.

Figure 6. *Theodoxus baeticus* (Lamarck, 1822). **A–C**. Paralectotype of *N. baetica* from Andalusia, Spain (MHNG-MOLL-51319). **D**) Operculum of a paralectotype of *N. baetica* from Andalusia (MHNG-MOLL-51319); **E–G**. Lectotype of *N. baetica* from Andalusia (MHNG-MOLL-51319); **H–J; K; L; M; N**. Five syntypes of *N. meridionalis* from Sicily (ZMB, without coll. no.); **O–R**. Topotype of *N. guadianensis* collected in the Guadiana River near Mértola, Portugal incorporated into the phylogeny (UGSB 22084); **S–V**. Specimen from Sóller, Balearic Islands used in the phylogeny (UGSB 19162). Scale bars: 1 mm.

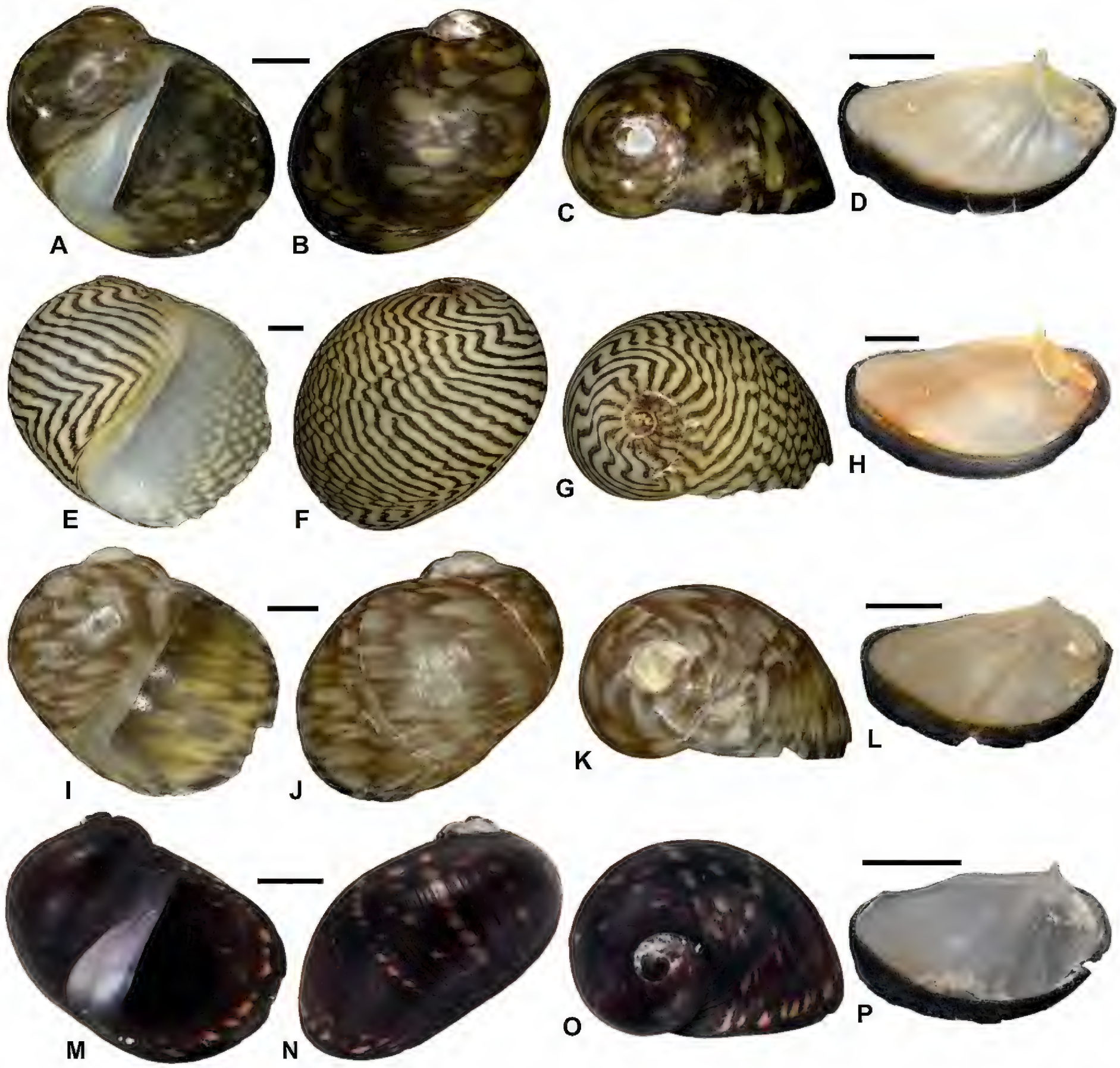

Figure 7. *Theodoxus baeticus* (Lamarck, 1822). **A–D**. Specimen (*T. callosus*-morphoype) collected in Akyaka, Turkey (UGSB 19118); **E–H**. Specimen (*T. callosus*-morphotype) collected in Káto Tragána, Greece (UGSB 2488); **I–L**. Specimen (*T. varius*-morphotype) collected at the Blue Eye Nature Monument, Albania (UGSB 24170); **M–P**. Specimen (*T. meridionalis*-morphotype) collected at the Ketana Oasis, Gabes, Tunisia (UGSB 18111). All specimens, except A–H, were used in the phylogeny (Fig. 2). Scale bars: 1 mm.

Theodoxus heldreichi: Welter-Schultes 2012: 28, unnumbered text figures.
Theodoxus saulcyi: Welter-Schultes 2012: 29, unnumbered text figures.
Theodoxus (*Theodoxus*) *euxinus*: Vinarski and Kantor 2016: 155.
Theodoxus (*Theodoxus*) *fluviatilis*: Vinarski and Kantor 2016: 154–155.
Theodoxus (*Theodoxus*) *subthermalis*: Vinarski and Kantor 2016: 157–158; Gürlek et al. 2019: 2993.

Type locality. Near Uppsala, Sweden.

Type material. Lectotype of *T. fluviatilis* are stored in LSL (coll. no. LSL.566; lectotype designated by Anistratenko et al. 1999; also see Anistratenko 2005). Syntypes of *N. saulcyi* are stored in MHNG (coll. no. MHNG-MOLL-111736). Seven syntypes of *T. fluviatilis* var. *subthermalis* are stored in MHNG (coll. no. MHNG-MOLL-11737). The type material of *T. heldreichi fluvicola* is stored in NSMF (coll. no. 309.439 and 309.440). Most taxa described by Lindholm are deposited in ZIN, including five syntypes of *N. fluviatilis* var. *cereoflava* (coll. no. 6055/1), three syntypes of *N. brauneri* (coll. no. 6046/1), one syntype of *N. brauneri* f. *alboguttata* (coll. no. 6051/1), two syntypes of *N. brauneri* f. *lacrymans* (coll. no. 6052/1), one syntypes of *N. brauneri* f. *pulcherrima* (coll. no. 6053/1), and three syntypes of *N. danubialis* var. *danasteri* (coll. no. 5910/3).

Remarks. *Theodoxus fluviatilis* exhibits considerable variation in periostracum colouration (Neumann 1959;

Figure 8. *Theodoxus baeticus* (Lamarck, 1822). **A–D**. Specimen from Cuquillo, Granada, Andalusia, Spain (UGSB 22089); **E–H**. Specimen (*T. meridionalis*-morphotype) collected in the Palancia River, Navajas, Spain (UGSB 22090); **I–L**. Specimen (*T. elongatulus*-morphotype) from Arrancada, Pombal, Portugal (UGSB 22080); **M–P**. Specimen (*T. velascoi*-morphotype) from Montanejos, Castellón, Spain (UGSB 22082). *Theodoxus* cf. *valentinus* (Graells, 1846). **Q–S**. Specimen conforming to *T. valentinus* from the Verd River, Masalavés, Spain (UGSB 21787); **T**. Operculum of a specimen conforming to *T. valentinus* from the same locality as Q–S (UGSB 22087). All specimens, except Q–S, were used in the phylogeny (Fig. 2). Scale bars: 1 mm.

Figure 9. *Theodoxus fluviatilis* (Linnaeus, 1758). **A–D**. Specimen collected close to Oued Laabid, Morocco (UGSB 18106) (Fig. 2); **E–H**. Specimen from the Danube River, Wörth an der Donau, Germany (UGSB 24173); **I–L**. Specimen (*T. euxinus*-morphotype) collected in the Papuç Creek, Kıyıköy, Turkey (UGSB 24172) (Fig. 2); **M–P**. Specimen (*T. euxinus*-morphotype) from Ovidiopol, Ukraine (UGSB 18124); **Q–S**. Specimen (*T. heldreichi*-morphotype) collected in Lake Eğirdir, Turkey (UGSB 20361); **T**, **U**. Specimen (*T. danasteri*-morphotype) collected in Krasna Kosa, Ukraine (UGSB 18417) (Fig 2); **V**. Opercula of a *T. danasteri*-morphotype from Lake Skadar, Montenegro (UGSB 24171). Specimens A–D, I–L and T–U were used in the phylogeny (Fig. 2). Scale bars: 1 mm.

Glöer and Pešić 2015). It is not surprising that molecular studies already support the synonymy of a number taxa such as *T. euxinus* (Clessin, 1886), *T. fluviatilis abrauensis* (Milaschewitsch, 1914) *T. danasteri* (Lindholm, 1908), and *T. subthermalis* Issel, 1865, and further suggest the inclusion of *T. saulcyi* (Bourguignat, 1852) (including *N. graeca* Westerlund, 1886, *T. ghigii* Gambetta, 1929; both listed as synonyms of *T. saulcyi* by Bank (2006)) and *T. heldreichi* (Martens, 1879) (Bunje and Lindberg 2007; Sands et al. 2019a). The above species share near identical operculum structures, with a strong rib-shield, rib-pouch and the absence of a pseudo-apophysis (Figs 9, 10), which were often disregarded in early *Theodoxus* species descriptions. Moreover, a number of taxa including *T.*

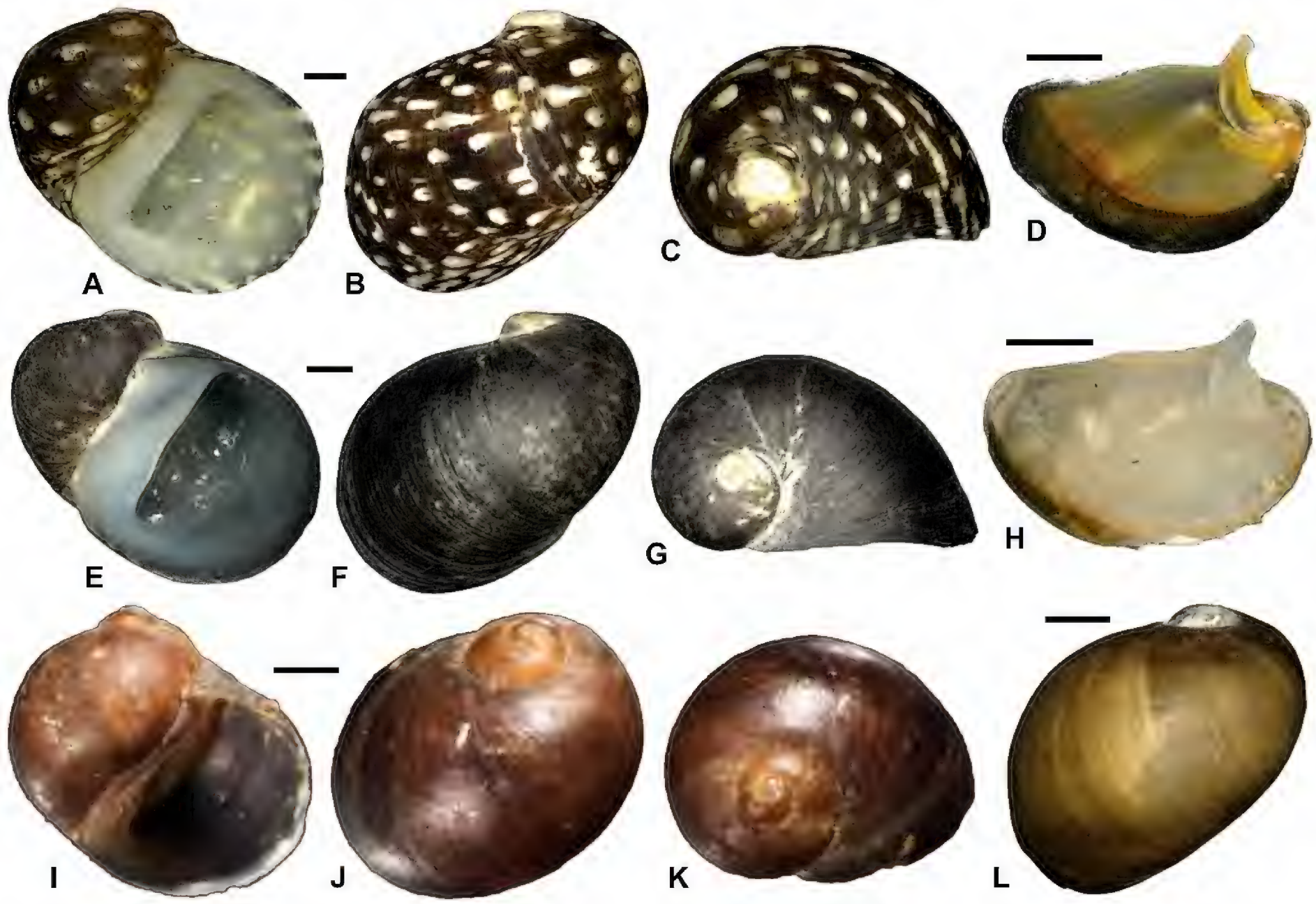

Figure 10. *Theodoxus fluviatilis* (Linnaeus, 1758). **A–D**. Specimen (conforming to *T. sarmaticus*) from the Dnieper-Bug estuary, Ukraine (UGSB 18328); **E–H**. Specimen (*T. subthermalis*-morphotype) from Novy Afon, Abkhazia, Georgia (UGSB 18402); **I–K**. Syntype of *N. saulcyi* from near the Penteli Monastery, Greece (MHNG-MOLL-111736); **L**. Specimen (*T. saulcyi*-morphotype) from Stilos, Crete, Greece (UGSB 20519) incorporated into the phylogeny (Fig. 2). Scale bars: 1 mm.

brauneri (Lindholm, 1908) (along with subspecies *T. b. alboguttatus* (Lindholm, 1908), *T. b. lacrymans* (Lindholm, 1908) and *T. b. pulcherrimus* (*Lindholm, 1908*)), *T. fluviatilis cereoflava* (Lindholm, 1913), and *T. dniestroviensis* Put', 1972 are well within the variability of *T. fluviatilis* and are considered junior synonyms herein as well.

Bunje and Lindberg (2007) also suggested *T. velox* V. Anistratenko in O. Anistratenko et al., 1999 as conspecific with *T. fluviatilis*. However, Sands et al. (2019a) found substantial differentiation on the molecular level, indicating a sister relation between *T. fluviatilis* and *T. velox* (also see Fig. 2). Although it may be challenging to differentiate these species morphologically in some instances, there appears to be a stronger callus on the operculum in *T. fluviatilis* and greater phenotypic plasticity in shell shape and periostracum colouration as compared to *T. velox* (Figs 9, 10, 22).

Distribution. *Theodoxus fluviatilis* is widely distributed across Europe, northern Africa, and western Asia. Records of this species and its synonyms are noted as far as Ireland to the West (Anderson 2005), Morocco in the South (Taybi et al. 2017), Sweden and Finland in the North (Kangas and Skoog 1978), and European Russia in the East (Vinarski and Kantor 2016). In addition, there are numerous records from across Anatolia (Schütt and Şeşen 1989b, 1992; Yıldırım et al. 2006; Gürlek et al. 2019) and Georgia (Vinarski and Kantor 2016) within the study region. The wide distribution range has been substantiated through molecular studies (Bunje 2005; Bunje and Lindberg 2007; Sands et al. 2019a; Fig. 3C). Some authors suggested that this species also occurs in Iran (Roth 1987; Glöer and Pešić 2012), but molecular analyses of material from these parts do not support this hypothesis (Sands et al. 2019a, 2019b; personal observation A.F.S.).

Theodoxus gloeri Odabaşı & Arslan, 2015

Figure 11A–C

Theodoxus gloeri Odabaşı and Arslan 2015: 329–330, fig. 2; Gürlek et al. 2019: 2993; Glöer 2019: 44, fig. 29.

Type locality. Balıkdamı Wetland-Sakarya River, Eskişehir, Turkey; 39.15277°N, 31.61562°E (Fig. 3D).

Type material. Holotype and seven paratypes are deposited in COMULM (coll. no. COMULM-G 0052-0053). Further nine paratypes are deposited in OGUHB (coll. no. OGUHB-01759). An additional paratype is stored in the private collection of one of us (coll. Glöer; Fig. 11A–C).

Remarks. *Theodoxus gloeri* Odabaşı & Arslan, 2015 shows strong similarity to the fossil species *T. pilidei* (Tournouër, 1879) from Romania and *T. lamelliferus* (Mi-

Figure 11. *Theodoxus gloeri* Odabaşı & Arslan, 2015. **A–C**. Paratype from Balıkdamı Wetland-Sakarya River, Eskişehir, Turkey (coll. Glöer). Scale bar: 1 mm.

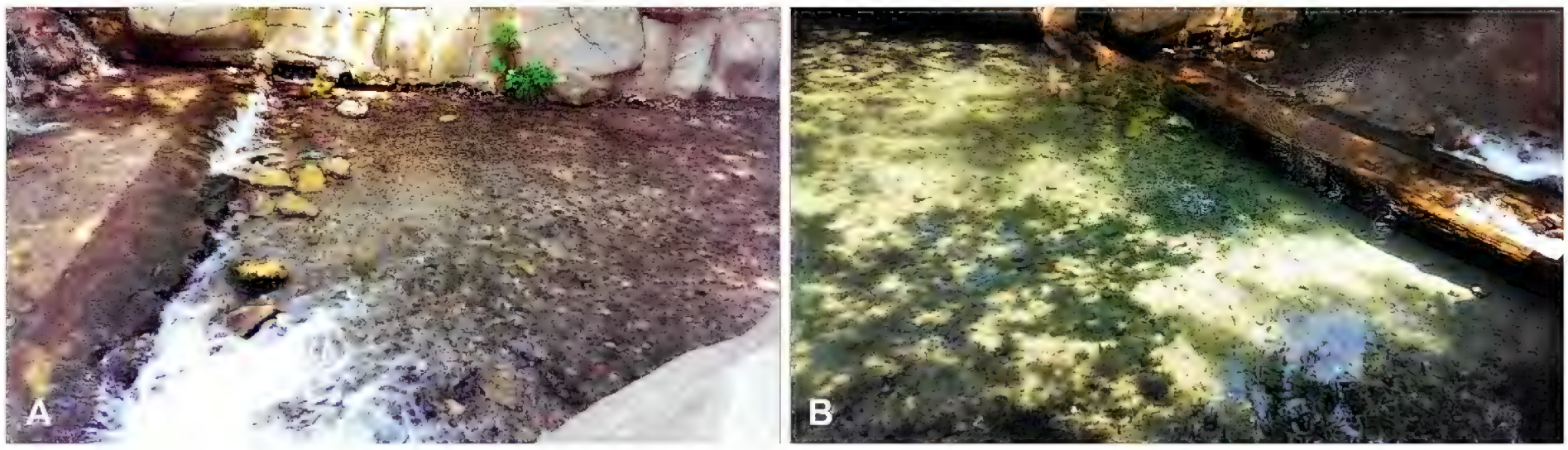

Figure 12. Type locality of *Theodoxus gurur* Sands & Glöer sp. nov. **A**, **B**. Suyunbaşı spring complex, Ayrancılar, İzmir, Turkey, 38.24826°N, 27.28117°E.

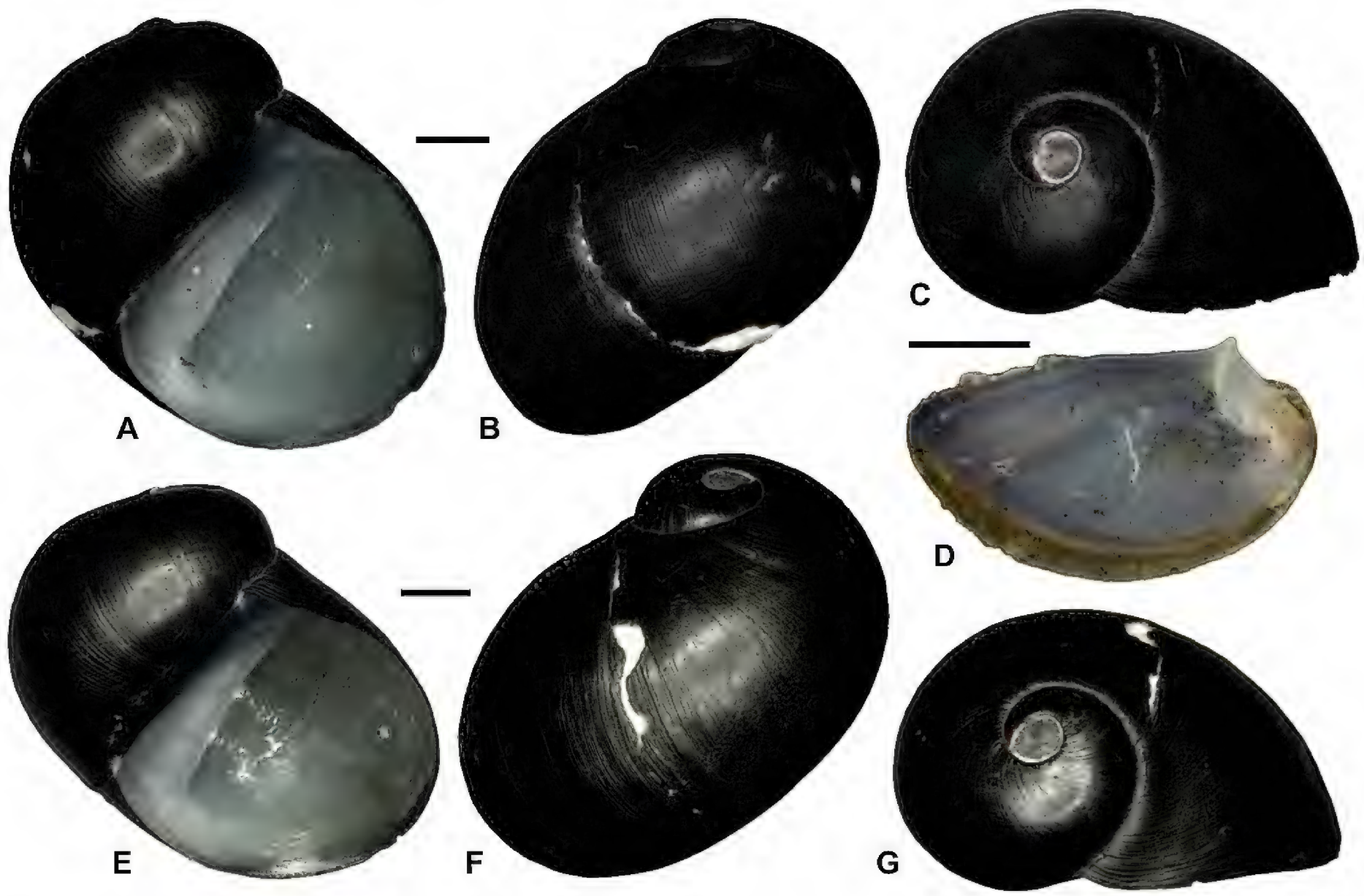

Figure 13. *Theodoxus gurur* Sands & Glöer sp. nov. **A–D**. Holotype from the Suyunbaşı spring complex, Ayrancılar, İzmir, Turkey stored in NMNL (RMNH.MOL.342197); **E–G**. Paratype from same locality and storage facility (RMNH.MOL.342199). Scale bars: 1 mm.

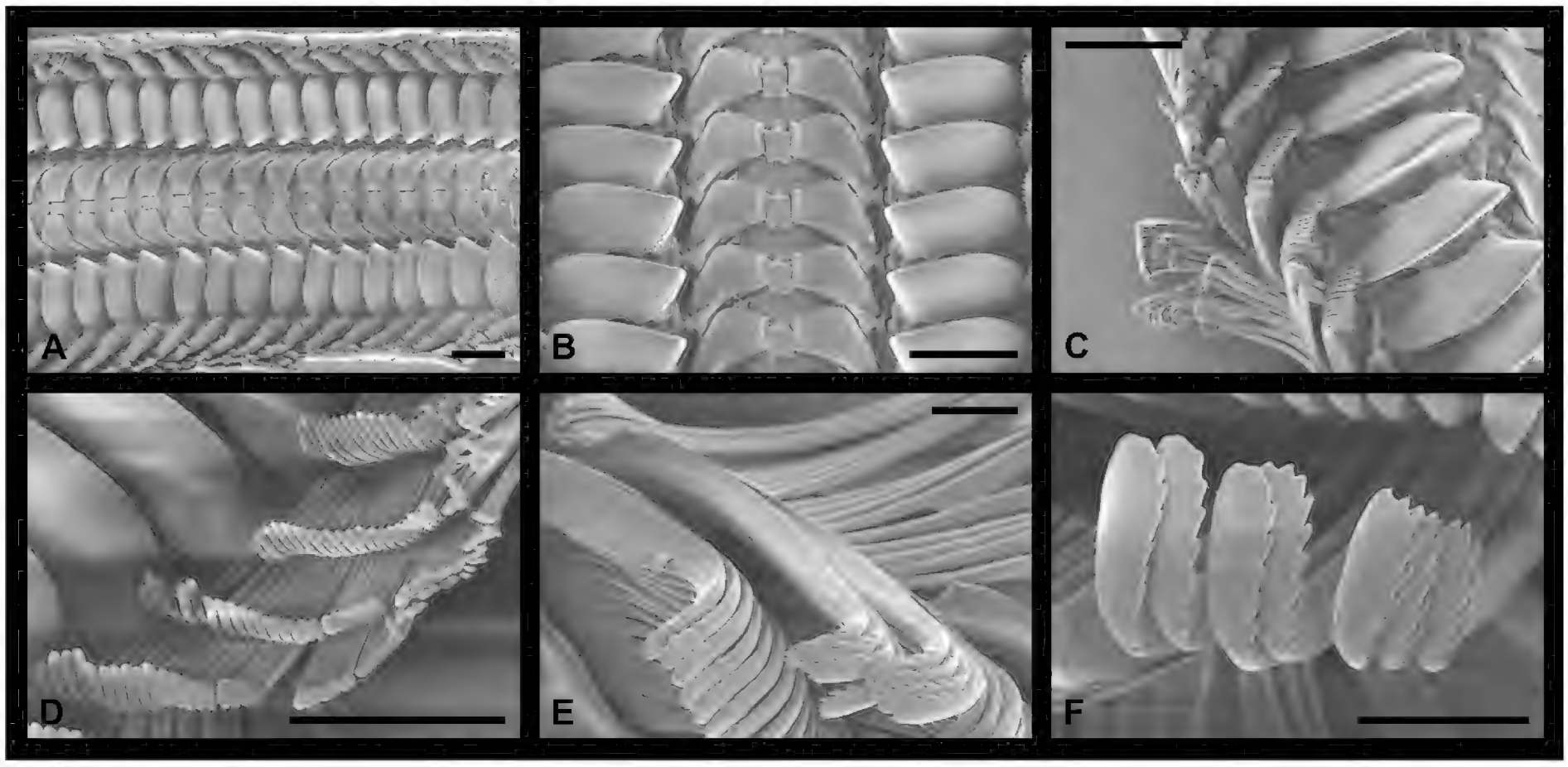

Figure 14. Radula of *Theodoxus gurur* Sands & Glöer sp. nov. paratypes (UGSB 20689). **A**. Portion of the radula showing full sets of teeth; **B**. Magnified view of the central and lateral teeth; **C**. Magnified view of the lateral and marginal teeth; **D**. Magnified view of the first row of marginal teeth; **E**. Merging point between the first and second rows of marginal teeth; **F**. Magnified view of the faces of inner marginal teeth belonging to the first row. Scale bars: 100 µm (A–D), 20 µm (E–F).

laschewitsch, 1912) from the Black Sea (near Alushta, Crimea) with strongly ribbed shells, but it is smaller than both (Odabaşı and Arslan 2015; Glöer 2019; Fig. 11). Although it is expected to be an extant subterranean species, no living material has ever been recorded and its phylogenetic position is presently unknown (Odabaşı and Arslan 2015).

Distribution. Only known from two sites in very close proximity within the Balıkdamı Wetland-Sakarya River, Eskişehir, Turkey (Odabaşı and Arslan 2015; Fig. 3D).

Theodoxus gurur Sands & Glöer, sp. nov.

http://zoobank.org/F2C8585A-1268-4436-9334-8B64AE20F6EE

Figures 12A, B, 13A–G, 14A–F

Type locality. Suyunbaşı spring complex, Ayrancılar, İzmir, Turkey; 38.24826°N, 27.28117°E (Figs 3A, 12A, B).

Holotype. RMNH.MOL.342197 (Suyunbaşı spring complex, Ayrancılar, İzmir, Turkey; 38.24826°N, 27.28117°E) stored in NMNL: Shell height 5.8 mm, width 6.0 mm (Fig. 13A–D).

Paratypes. Twenty four specimens from Suyunbaşı spring complex, Ayrancılar, İzmir, Turkey; 38.24826°N, 27.28117°E: 11 in NMNL (RMNH.MOL.342198, RMNH.MOL.342199; Fig. 13E–G) and 13 in UGSB (UGSB 20689, UGSB 20745, UGSB 20746; Fig. 14A–F).

Etymology. The word "gurur" means "pride" in Turkish, referring to the PRIDE (Drivers of Pontocaspian Biodiversity Rise and Demise) programme (also see Acknowledgements). One of its aspects is understanding the evolution of mollusc species in the Pontocaspian and associated satellite regions in Anatolia and the Balkans.

Description. Shell (Fig. 13A–C, E–G): Hemispherical, transversely slightly elongate, consisting of typically 3–3.5 whorls that rapidly grow. Spire of low to moderate height for *Theodoxus*; apex often corroded. Shell height ranges from 5–6.5 mm, width from 5.3–7.0 mm. Periostracum uniformly black; surface can be glossy, always finely striated with growth lines. Aperture semicircular; no serrations on the inner lip. Columellar plate smooth, flat to slightly concave, inclined towards aperture; blue-grey in colour.

Operculum (Fig. 13D): Operculum plate made of two parts, calcareous base and conchioline lamella; calcareous base mostly light to dark brown; lamella light yellow-orange. Left adductor of operculum base slightly triangulate, no obvious callus on top right edge. Apophysis distinctively white; broader at top, narrower and attenuated at bottom. Rib-shield strong. Small, short rib-pouch. Small white pseudo-apophysis extends from base of apophysis.

Radula (Fig. 14A–F): R-central tooth flanked by the A-central, B-central, C-central, E-lateral on each side. Additionally, two interconnected layers of marginal teeth occur, encasing central and lateral teeth. R-central with nearly rectangular face, slightly concave anterior edge. A-central large and flat with thin ridge; some curling of ridge on upper edge of cusp. B-central diminished, forms irregular "S" shape. C-central equally diminished, partly hidden below lower edge of E-lateral. E-lateral simple, with no serration on upper edge. First layer of marginal teeth comprises 35–37 teeth, which decrease in size away from E-lateral but increase in size and show serrations on edges of small faces; semidetached from second layer, which is fused and forms outer wall.

Differentiating features. Using only conchological features of periostracum colouration and patterning and

shell shape, the hemispherical, glossy black, and finely striated shells of *T. gurur* sp. nov. are easily differentiable from *T. altenai*, which displays light ivory spots on a dark brown-black background (Figs 4A–G, 13A–G), and *T. gloeri*, which lacks shell pigmentation and bears strong axial ribs on the shell (Figs 11A–C, 13A–G). However, it is still challenging to differentiate *T. gurur* sp. nov. from some morphotypes of *T. anatolicus*, *T. baeticus*, *T. fluviatilis*, *T. jordani*, *T. macri* (G.B. Sowerby II, 1849), *T. major* Issel, 1865, *T. pallidus* (Dunker, 1861), *T. syriacus* (Bourguignat, 1852), *T. velox*, *T. wesselinghi* sp. nov., and *T. wilkei* sp. nov., which can share hemispherical, glossy black, and finely striated shells (Figs 5A–M, 6A–G, 8A–D, 10E–H, 13A–G, 15P–R, 16C–E, O, P, 18A–D, 19O, P, 20A–D, 21I–R, 22I, J, 24H–J, 27A–D). *Theodoxus gurur* sp. nov. can be distinguished from Anatolian morphotypes of *T. baeticus*, which typically displays ivory blotches on brown background (Fig. 7A–D); *T. jordani*, which typically displays brown diagonal zig-zag line patterning on an ivory background (Fig. 15E–L) and *T. velox*, which tends to have white-ivory stripes on a dark background (Fig. 22K–M). Moreover, *T. jordani* typically has a lighter columellar plate in comparison (Figs 13, 15–17). Finally, the light to dark brown calcareous base of the operculum in *T. gurur* sp. nov. can help to distinguish it from *T. altenai*, *T. anatolicus*, *T. baeticus*, *T. jordani*, *T. macri*, *T. major*, *T. pallidus*, *T. syriacus*, and *T. wesselinghi* sp. nov., which typically have lighter calcareous bases ranging from ivory to cream or light brown (Figs 4–8, 13, 15–21, 24); *Theodoxus wilkei* sp. nov., differs in its bright orange operculum (Figs 13, 27).

More differentiating features occur in the structure of the operculum. These include the attenuated apophysis in *T. gurur* sp. nov. (Fig. 13), which is lacking or reduced in *T. altenai* and *T. jordani* (Figs 4, 15, 17). The lack of or an extremely diminished rib-pouch and rib-shield in *T. altenai*, *T. anatolicus*, *T. jordani*, and *T. macri* separate these species from *T. gurur* sp. nov. (Figs 4, 5, 13 15, 17, 18). Additionally, the presence of a pseudo-apophysis differentiates *T. gurur* sp. nov. from *T. fluviatilis*, *T. major*, *T. pallidus*, *T. syriacus*, *T. velox*, *T. wesselinghi* sp. nov., and *T. wilkei* sp. nov. (Figs 9, 10, 13, 19–22, 24, 27). *Theodoxus anatolicus*, *T. baeticus*, *T. jordani*, and *T. macri*, in turn, appear to have overall larger pseudo-apophyses (Figs 5–8, 13, 15, 17, 18). Finally, the presence of a strongly defined callus on the top edge of the right adductor in *T. altenai*, *T. anatolicus*, *T. baeticus*, *T. fluviatilis*, *T. pallidus*, *T. syriacus*, *T. wesselinghi* sp. nov., and *T. wilkei* sp. nov. may help in differentiation from *T. gurur* sp. nov. (Figs 4–10, 13, 20, 21, 24, 27). Also, the more angulated left adductor of the operculum base of this species differs from the rounded left adductor seen in *T. syriacus*, *T. wesselinghi* sp. nov., and *T. wilkei* sp. nov. (Figs 13, 27).

Little is known about the radula of many recognised *Theodoxus* spp. Based on the available data, *T. gurur* sp. nov. can be distinguished by the rectangular face of the R-central from *T. fluviatilis*, *T. jordani*, *T. wilkei* sp. nov., and *T. wesselinghi* sp. nov., which have more square, triangulate or globular faces in comparison (see Baker 1923; Zettler 2008; Figs 14B, 25B, 28B). The smooth upper edge of the E-lateral can be used to distinguish *T. gurur* sp. nov. from *T. wilkei* sp. nov. and *T. major*, which generally have large serrations (see Anistratenko et al. 2017; Fig. 14B, C).

Remarks. Our results, as well as the phylogeny of Sands et al. (2019a), suggest *T. gurur* sp. nov. belongs to a large clade of Anatolian and Mediterranean species that includes *T. altenai*, *T. anatolicus*, *T. baeticus*, *T. jordani*, *T. macri*, *T. marteli*, and an undescribed species from Spain (Sands et al. 2019a; Fig. 2). The *T. gurur* sp. nov. lineage likely diverged from these species during the Pliocene (Fig. 2).

Distribution. Only known from the type locality (Figs 3A, 12A, B).

Ecology. The Suyunbaşı spring complex is part of a recreational park that has been heavily altered to channel and pool water for recreational activities (personal observation M.E.G.). The spring floor and channels are made up of a number of small to large stones or coarse sand, while macrophytes are largely absent (Fig. 12A, B). *Theodoxus gurur* sp. nov. can be found attached to stones and concrete banking and co-occurs with *Pseudamnicola* sp. (personal observation M.E.G.).

Theodoxus jordani (G.B. Sowerby I, 1836)

Figures 15A–V, 16A–P, 17A–J

Neritina Jordani G.B. Sowerby I 1836: 4, pl. 99, fig. 49; G.B. Sowerby II 1849: 531, pl. 115, figs 213–215; Bourguignat 1853: 69; Martens 1879: 84–86, pl. 2, figs 14–16; Kobelt 1899: 2–3, pl. 211, fig. 1319 (as "*N. jordanica*" in figure caption).

Neritina Michonii Bourguignat 1852: 25; Bourguignat 1853: 70, pl. 2, figs 48–51.

Neritina Bellardii Mousson 1854: 52–53.

? *Neritina Africana* Reeve 1856: pl. 30, fig. 138a, b.

Neritina Nilotica Reeve 1856: pl. 34, fig. 157a, b; Martens 1879: 82–83, pl. 2, figs 17–19, pl. 13, figs 14–16; Kobelt 1899: 2, pl. 211, fig. 1317.

Neritina Jordani var. *turris* Mousson 1861: 151–152; Kobelt 1899: 3, pl. 211, fig. 1320.

Neritina Karasuna Mousson 1874: 34–35; Blanckenhorn 1897: 101–102, pl. 8, figs 6–8.

Neritina meridionalis var. *Mesopotamica* Mousson 1874: 35.

Neritina Euphratica Mousson 1874: 49; Kobelt 1899: 2, pl. 211, fig. 1318.

Neritina Anatolica var. *Mesopotamica*: Martens 1874: 33–34, pl. 5, fig. 42.

Neritina cinctella Martens 1874: 34, pl. 5, fig. 43; Martens 1879: 91, pl. 13, figs 22–24; Kobelt 1899: 4–5, pl. 211, fig. 1326.

Neritina Macrii [sic]: Martens 1879: 88–90, pl. 4, figs 11–13, pl. 13, figs 27–29 (**non** *Neritina macri* G.B. Sowerby II, 1849; partim, non pl. 13, fig. 13).

Neritina Mesopotamica: Martens 1879: 90, pl. 13, figs 20, 21; Kobelt 1899: 4, pl. 211, fig. 1325.

Neritina (*Theodoxia*) *Jordani* var. *aberrans* Dautzenberg 1894: 351.

Neritina Orontis Blanckenhorn 1897: 101, pl. 8, figs 3–5.

Theodoxia Macrii [sic]: Germain 1921: 516–518 (**non** *Neritina macri* G.B. Sowerby II, 1849).

Theodoxia jordani: Germain 1921: 511–514.

Neritina Ponsoti Pallary 1930: 286–287, fig. 1.

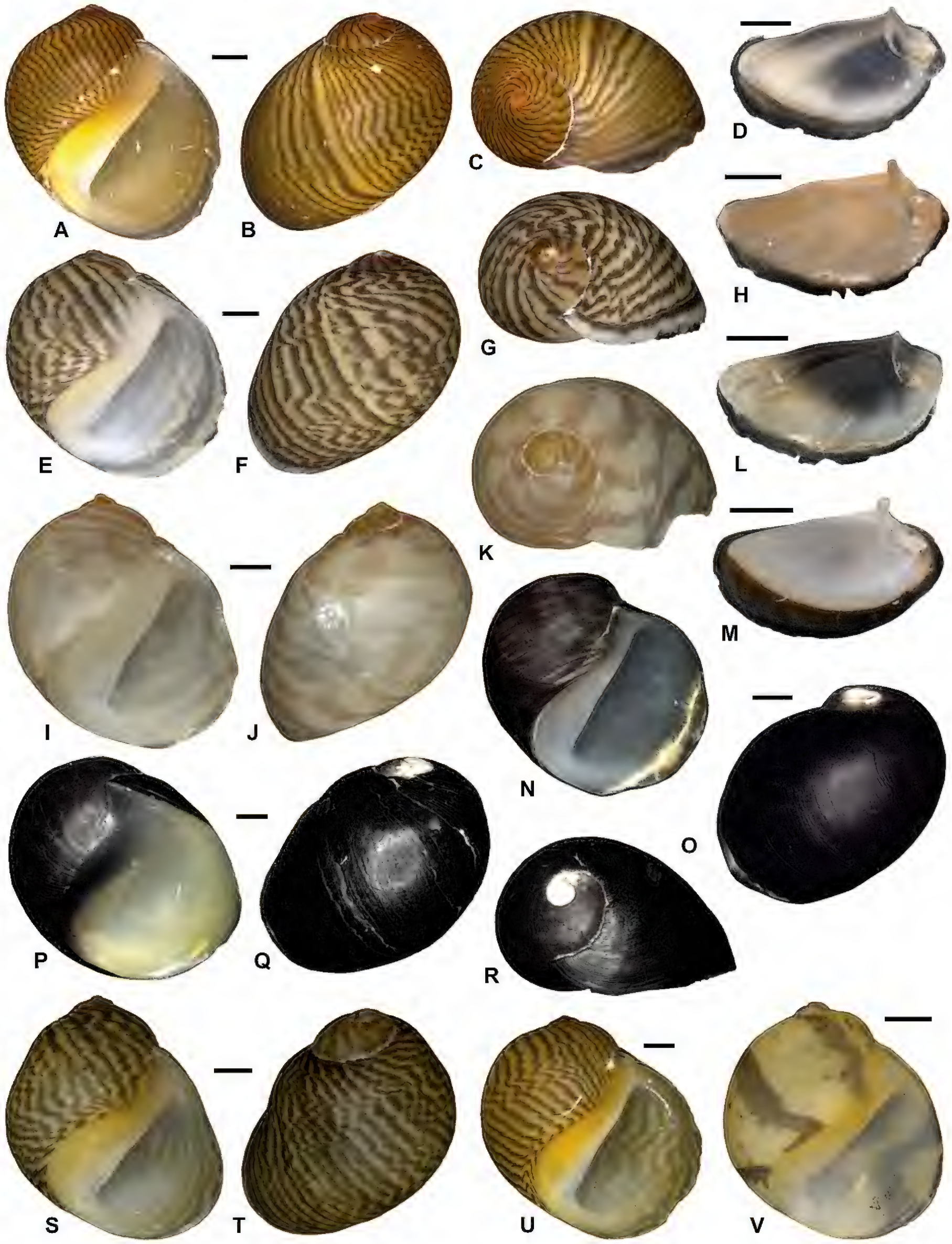

Figure 15. *Theodoxus jordani* (G.B. Sowerby I, 1836). **A–D**. Specimen from the Avakas Gorge, Peyia, Cyprus (UGSB 18321) incorporated into the phylogeny (Fig. 2); **E–H**. Specimen collected in the Ceyhan River, Eski Misis, Adana, Turkey (UGSB 20777); **I–L**. Specimen from the Orontes River, Antakya, Hatay, Turkey (UGSB 24175) used in the phylogeny (Fig. 2); **M–O**. Specimen (*T. euphraticus*-morphotype) from the Seyed Hosein Park spring, near the Bishapur, Fars, Iran (UGSB 22233); **P–R**. Topotype of *N. jordani* from the River Jordan, Israel (UGSB 24177) incorporated into the phylogeny (Fig. 2); **S**, **T**. Specimen (*T. euphraticus*-morphotype) from the Karun River, Ahvaz, Iran (UGSB 21681); **U**. Specimen (*T. niloticus*-morphotype) collected in the Nile River, Egypt (UGSB 24178) used in the phylogeny (Fig. 2); **V**. Specimen (*T. euphraticus*-morphotype) from the Karun River, Ahvaz, Iran (UGSB 21682). Scale bars: 1 mm.

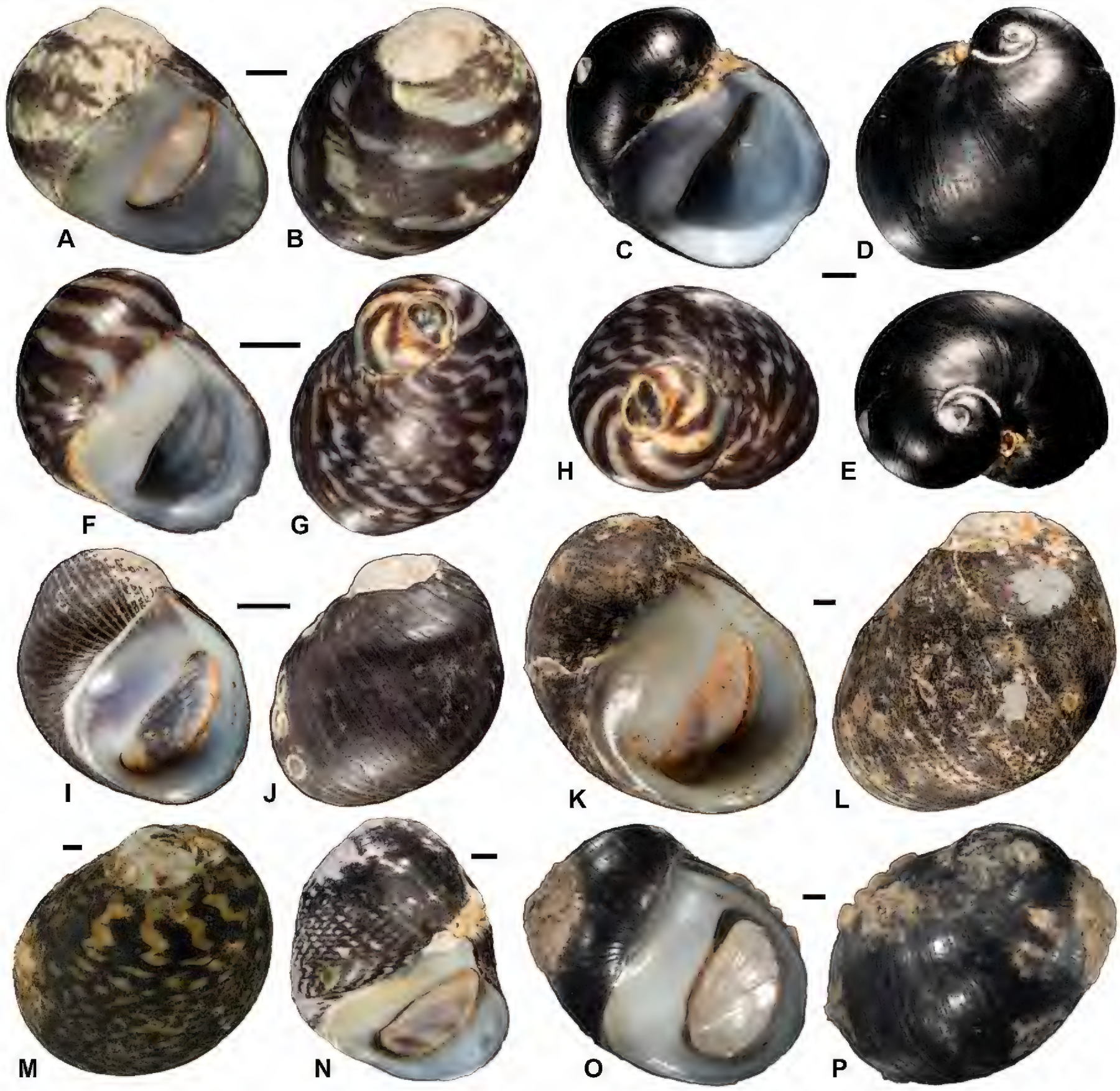

Figure 16. *Theodoxus jordani* (G.B. Sowerby I, 1836). **A**, **B**. Syntype of *N. euphratica* from the Euphrates River at Samawah, Iraq (ZMZ 528916); **C–E**. Syntype of *N. michonii* from Syria (MHNG-MOLL-111706); **F–H**. Syntype of *N. karasuna* collected from the Karasu River, south-eastern Turkey (ZMZ 528937); **I**, **J**; **K**, **L**. Two syntypes of *N. ponsoti* from Lake Muzayrīb, Syria (MNHN-IM-2000-32754); **M**. Syntype (labelled as paratype) of *N. ponsoti* from Lake Muzayrīb (MT820, RBINS); **N**. Syntype of *N. jordani* var. *turris* collected in the Sea of Galilee (ZMZ 528930); **O**, **P**. Syntype of *N. bellardii* from the Litani River, Beqaa valley, Lebanon (ZMZ 528918). Scale bars: 1 mm.

Theodoxus (*Neritaea*) *jordani* var. *unicarinatus* Picard 1934: 107–111, pl. 7, figs 1–4.

Theodoxus (*Neritaea*) *jordani* var. *bicarinatus* Picard 1934: 111–112, pl. 7, figs 5–8.

Neritina (*Neritaea*) *Gombaulti* Pallary 1939: 107, pl. 4, figs 53–56.

Neritina (*Neritaea*) *homsensis* Pallary 1939: 108, pl. 4, figs 57–61.

Neritina (*Neritaea*) *homsensis* var. *major* Pallary 1939: 109 (**non** *Neritina wallisiarum* var. *major* Récluz, 1850).

Neritina (*Neritaea*) *homsensis* var. *minor* Pallary 1939: 109 (nomen nudum, **non** *Neritina minor* Menke, 1828).

Neritina (*Neritaea*) *Ponsoti*: Pallary 1939: 109–110, pl. 4, figs 44–46.

Theodoxus (*Neritaea*) *jordani*: Tchernov 1975: 153; Schütt and Ortal 1993: 78–79, pl. 3, figs 37–41; Bandel 2001: 84–86, figs 12–20, 32–40; Amr and Abu Baker 2004: 221–222, fig. 1.

Theodoxus (*Neritaea*) *cinctella*: Schütt and Şeşen 1989a: 56–57.

Theodoxus (*Neritaea*) *cinctellus*: Schütt and Şeşen 1989b: 45–46; Yıldırım 1999: 886.

Theodoxus (*Neritaea*) *jordani tricarinatus* Schütt in Schütt and Ortal 1993: 79, pl. 3, fig. 42.

Theodoxus (*Neritaea*) *pliocostulatus* Schütt in Schütt and Ortal 1993: 79–80, pl. 3, fig. 43.

Theodoxus niloticus: Brown 1994: 45, figs 16b–c.

Theodoxus jordani: Yıldırım 1999: 886; Gürlek et al. 2019: 2993; Glöer 2019: 44, figs 30.

non *Neritina mesopotamica*: Mansoorian 2001: 4, figs 1–4 (= *Neritina schlaeflii* Mousson, 1874).

Theodoxus macrii [sic]: Amr and Abu Baker 2004: 222, fig. 2; Handal et al. 2015: 25–26, fig. 1B (**non** *Neritina macri* G.B. Sowerby II, 1849).

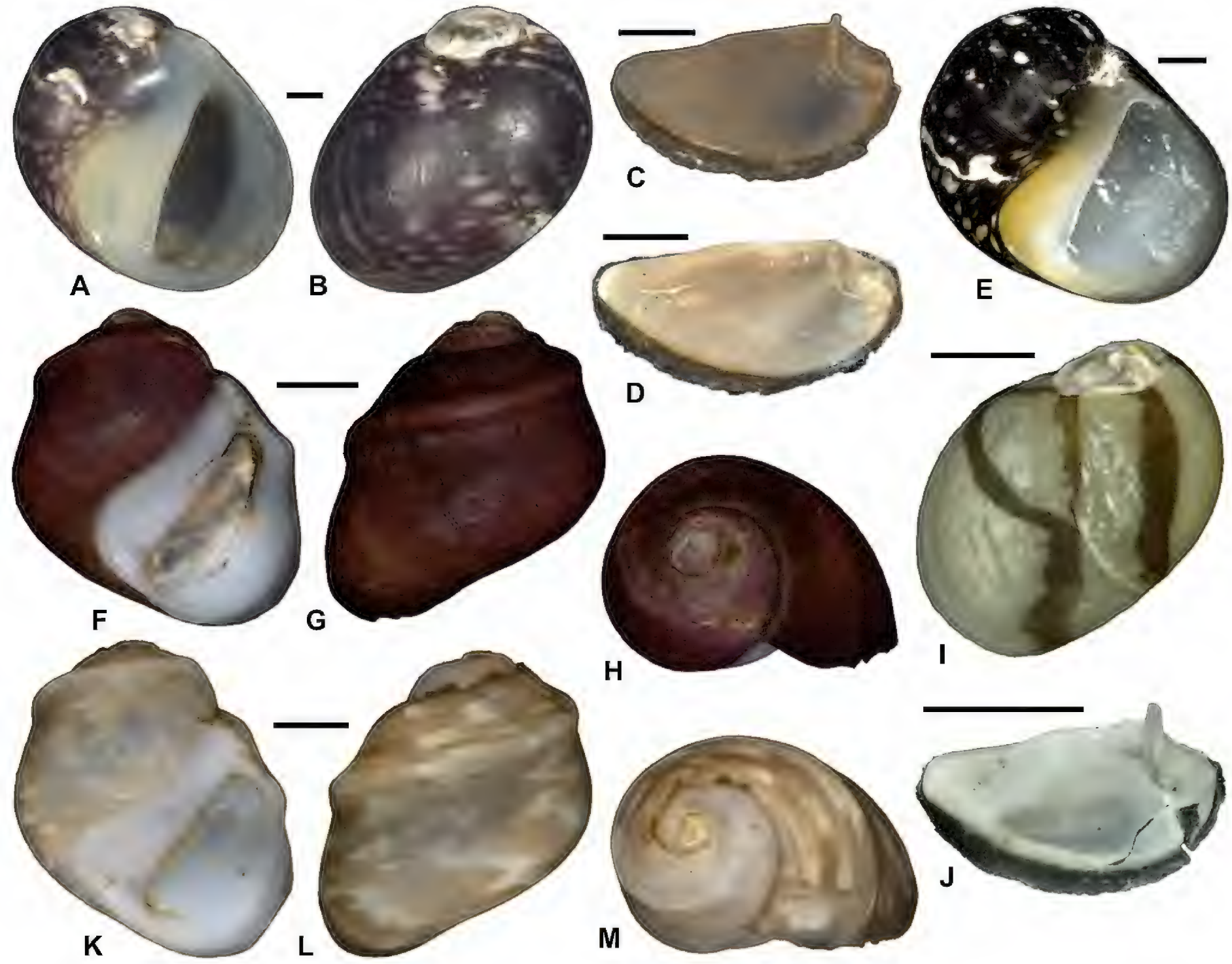

Figure 17. *Theodoxus jordani* (G.B. Sowerby I, 1836). **A–C**. Syntype of *N. meridionalis* var. *mesopotamica* from near Diyarbakır, Turkey (ZMZ 528914); **D**, **E**. Specimen (*T. mesopotamicus*-morphotype) collected in Şanlıurfa, Turkey (UGSB 23426) and used in the phylogeny (Fig. 2); **F–H**; **K–M**. Two syntypes of *N. cinctella* collected at the source of River Chabur near Ras al-Ayn, Syria (ZMB/Moll 21732); **I**, **J**. Topotype of *N. cinctella* from the same locality (UGSB 18762). Scale bars: 1 mm.

? *Neritina cinctellus*: Glöer and Pešić 2012: 13–14, fig. 2a, c.

? *Neritina mesopotamica*: Glöer and Pešić 2012: 14–16.

Theodoxus euphraticus: Mansoorian and Samaee 2012: 50–57 (partim, only material from Chaharmahal and Bakhtiari, Fars, Kermanshah, and Khuzestan provinces).

Neritina euphratica Glöer and Pešić 2012: 16, fig. 2d, e.

Theodoxus cf. *jordani*: Alhejoj and Bandel 2013: 146–147, pl. 1, figs 5–8.

Theodoxus octagonus Eichhorst 2016: 940, pl. 293, figs 1–8.

Theodoxus (*Neritaea*) *octagonus*: Mienis and Rittner 2017: 37, figs 1–3.

Theodoxus mesopotamicus: Glöer 2019: 47, fig. 34.

Theodoxus cinctellus: Gürlek et al. 2019: 2993.

Type locality. River Jordan.

Type material. The type material of *N. jordani* could unfortunately not be traced. The type material of the taxa introduced by Mousson are stored in ZMZ, including 16 syntypes of *N. bellardii* (coll. no. 528918), 13 syntypes of *N. euphratica* (coll. no. 528916), 20 syntypes of *N. jordani* var. *turris* (coll. no. 528930), 5 syntypes of *N. karasuna* (coll. no. 528937), and 56 syntypes of *N. meridionalis* var. *mesopotamica* (coll. no. 528912–528914). Additionally, 64 syntypes of *N. cinctella* are stored in ZMB (coll. no. ZMB/Moll 21732, 21735, 66639), 2 syntypes of *N. michonii* are stored in MHNG (MHNG-MOLL-111706–111707), 2 syntypes of *N. ponsoti* are stored in MNHM (coll. no. MNHN-IM-2000-32754) and another one (labelled as "paratype") is stored in RBINS (coll. no. MT820), and the holotype and two paratypes of *T. octagonus* are stored in BMSM (coll. no. BMSM 93544–93545).

Remarks. A number of nominal species have already been synonymised under *T. jordani* based on similarities in shell morphology and overlapping distribution ranges. These include *N. michonii* Bourguignat, 1852, *N. karasuna* Mousson, 1874, and *N. orontis* Blanckenhorn, 1897 (Martens 1879, Alhejoj et al. 2017). Moreover, Sands et al. (2019a) suggested that *T. niloticus* (Reeve, 1856) from the Nile River, Egypt (which has been considered a potential synonym of *N. africana* Reeve, 1856; Brown 1994) is conspecific with *T. jordani* on the basis of molecular data—something additionally supported by Glöer (2019). Our phylogenetic analyses expand upon this; we

show that *T. mesopotamicus* (including the synonyms *N. cinctella* Martens, 1874, *N. anatolica* var. *mesopotamica* Martens, 1874 (Schütt and Şeşen 1989a, 1989b), and *T. euphraticus* should be considered conspecific with *T. jordani* (Fig. 2). These results support the earlier notion of Roth (1987), who suggested that *T. euphraticus*, *T. jordani*, *T. mesopotamicus*, and *T. niloticus* may be conspecific based on morphological similarities, particularly concerning the opercula (Figs 15–17).

Although no molecular data could be incorporated, we further synonymise *T. octagonus* Eichhorst, 2016 with *T. jordani*. While *T. octagonus* maintains a subterranean lifestyle, the species shares a number of characteristics with *T. jordani* besides overlapping ranges; the operculum structures of the two species are near identical with otherwise large pseudo-apophyses and both occasionally show keeling of the shell. Moreover, key characters used to distinguish *T. octagonus*, such as the pronounced aperture and colouration of the shells, may be mitigated when intraspecific phenotypic plasticity of both species is considered (Heller 1979; Bandel 2001; Amr et al. 2014; Eichhorst 2016; Mienis and Rittner 2017; Figs 15–17). Likewise, the taxa *N. bellardii* Mousson, 1854, *N. jordani* var. *turris* Mousson, 1861, *N. ponsoti* Pallary, 1930, *N. homsensis* Pallary, 1939, *T. jordani* var. *unicarinatus* Picard, 1934, *T. jordani* var. *bicarinatus* Picard, 1934, *N. gombaulti* Pallary, 1939, *T. jordani tricarinatus* Schütt in Schütt & Ortal, 1993, and *T. pliocostulatus* Schütt in Schütt & Ortal, 1993 are well within the variability of *T. jordani* and are considered junior synonyms herein as well.

Regarding the phylogenetic placement of *T. jordani*, Bunje and Lindberg (2007) found *T. jordani* to form a sister species to *T. baeticus*. Sands et al. (2019a) reaffirmed this clade but found further support for a number of other species not included by Bunje and Lindberg (2007), including *T. macri*, which Sands et al. (2019a) found to be the closest sister species to *T. jordani* (also see Fig. 2). *Theodoxus jordani* and *T. macri* likely diverged in the early Pleistocene (Sands et al. 2019a; Fig. 2).

Notes on synonymy and homonymy: Martens (1874) described two taxa from the Chabur River near Ras al-Aynin Syria, *Neritina cinctella* Martens, 1874 and *Neritina anatolica* var. *mesopotamica* Martens, 1874. The latter variety is a junior homonym of *N. meridionalis* var. *mesopotamica* Mousson, 1874, which was published earlier (see also the discussion in the postface of Martens 1874 and Martens 1879). Based on newly collected material, Schütt and Şeşen (1989a, 1989b) considered all three taxa (*Neritina cinctella*, *N. anatolica* var. *mesopotamica*, and *N. meridionalis* var. *mesopotamica*) to belong to the same species given multiple intermediate forms. Although they were aware of the homonymy issue and that Mousson's name has priority, they erroneously chose *T. cinctellus* as the name of the species.

Distribution. *Theodoxus jordani* is common throughout southern Anatolia, the Levant, Mesopotamia, and parts of the Middle East, extending to at least southern Iran, although it is probably not found eastward of the Zagros Mountains (Roth 1987; Schütt and Şeşen 1989b; Bandel 2001; Sands et al. 2019a; Fig. 3A). It is also present on Cyprus and in the Nile River system, Egypt (Sands et al. 2019a). Some records of this species from Iran and Iraq (e.g. *N. mesopotamica* sensu Mansoorian 2001) may be misidentifications of *N. schlaeflii* Mousson, 1874 which inhabits the lower reaches of the Euphrates, Karun, and Tigris rivers, as well as other brackish water systems around the Persian Gulf (Glöer and Pešić 2012).

Theodoxus macri (G.B. Sowerby II, 1849)

Figure 18A–H

Neritina Macri G.B. Sowerby II 1849: 531, pl. 116, fig. 222.

Neritina Macrii [sic]: Martens 1879: 88–90, pl. 13, fig. 13 (partim, non pl. 4, figs 11–13, pl. 13, figs 27–29); Blanckenhorn 1889: 81 (synonymy tentative); Kobelt 1899: 5, pl. 212, figs 1327, 1328 (partim, excluding synonyms).

non *Theodoxia Macrii* [sic]: Germain 1921: 516–518.

non *Theodoxus macrii* [sic]: Amr and Abu Baker 2004: 222, fig. 2; Handal et al. 2015: 25–26, fig. 1B.

? *Theodoxus macrii* [sic]: Glöer 2019: 46, fig. 32.

Type locality. Asia Minor (= Anatolia).

Type material. According to Dance (1966), most material described by G.B. Sowerby II is deposited in BMNH, and parts also in the Tomlin Collection of NMW. Unfortunately, the types could not been located in either of these two institutions (A. Salvador, H. Wood pers. comm. 07/2018).

Remarks. The identity of this species is doubtful at the moment. G.B. Sowerby II (1849) based it on a black periostracum, oval shell, and a grey, more inclined columellar plate. The short description and sole figure, as well as the imprecise locality information ("Asia Minor") and the apparent lack of type material, render an attribution of newly collected specimens to that species uncertain. Sands et al.'s (2019a) material from eastern Cilicia and south-east Anatolia fit well in terms of shell shape and periostracum colouration, and we tentatively consider them to belong to *T. macri* (Fig. 18). The previous perception of *T. macri* was a different one though. In the literature of the late 19th century, it has been commonly considered a more widely distributed Middle Eastern species, with the junior synonyms *N. karasuna* and *N. michonii* (Martens 1879, Westerlund 1886, Kobelt 1899). More recently, Dagan (1971), Tchernov (1975), and Bandel (2001) considered *T. macri* a junior synonym of *T. jordani*, but based only on material from Israel and Jordan. Molecular analyses suggest that *Theodoxus* from Jordan, Israel, and Palestine belong to a single species, *T. jordani*, which is distinct from all other species (Sands et al. 2019a; Fig. 2). Although the true identity of *T. macri* remains dubious at the moment, these results indicate that *T. macri* does not occur outside of Cilicia and south-eastern Anatolia. Probably all previous records of *T. macri* from the Middle East (e.g. Najim 1959; Elkarmi and Ismail 2006; Handal et al. 2015) refer to *T. jordani*. If this

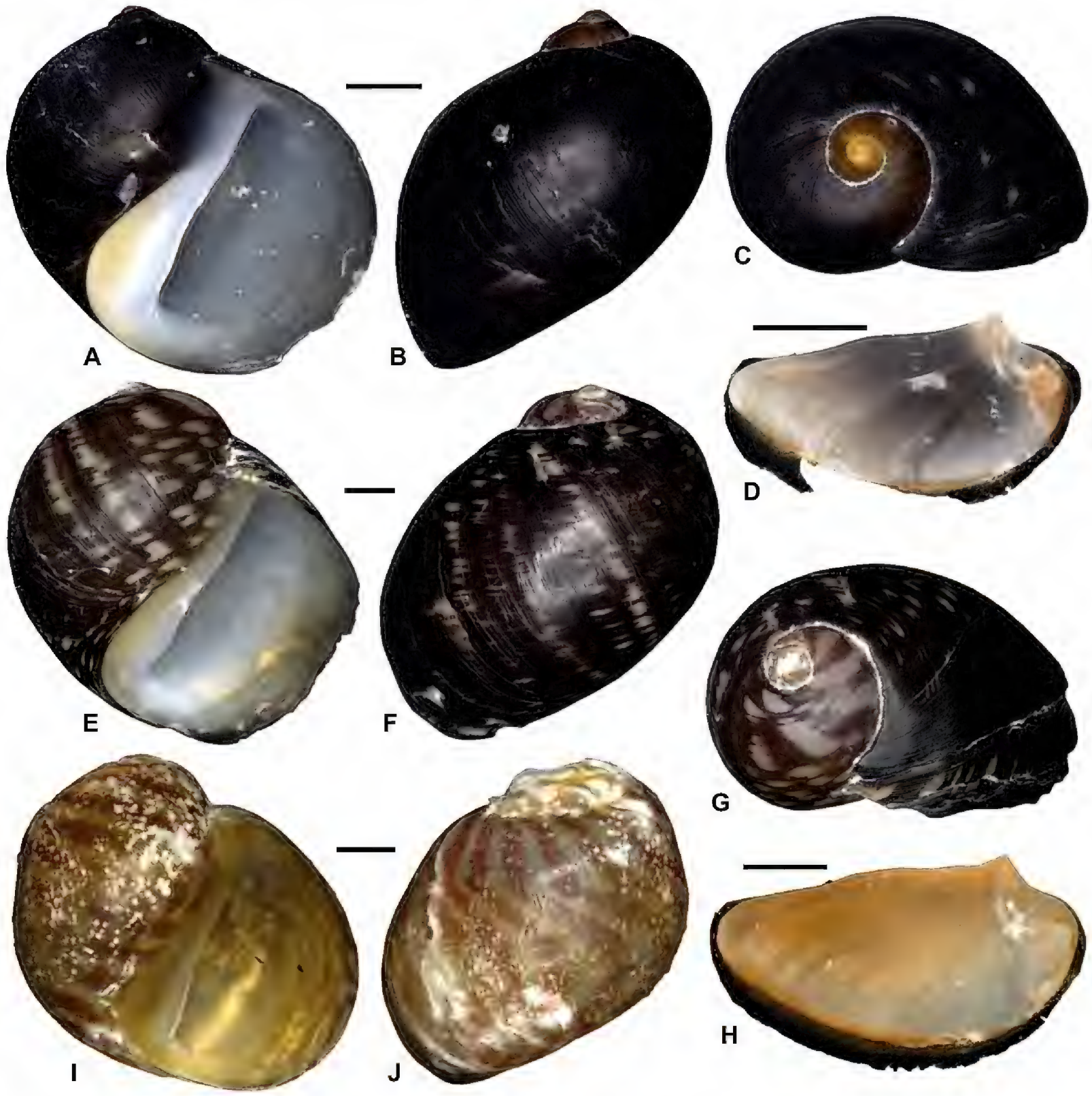

Figure 18. *Theodoxus macri* (G.B. Sowerby II, 1849). **A–D**. Specimen collected close to Harbiye Falls, Harbiye, Antakya, Turkey (UGSB 24179); **E–H**. Specimen from Lake Yenişehir, Reyhanlı, Turkey (UGSB 24180); **I**, **J**. Specimen from Lake Balık, Adalar, Turkey (UGSB 24181). All specimens (A–J) were used in the phylogeny (Fig. 2). Scale bars: 1 mm.

is corroborated, *T. macri* likely diverged from a common ancestor with *T. jordani* in the early Pleistocene (Sands et al. 2019a; Fig. 2).

Note on authority: G.B. Sowerby II (1849) attributed the name to Récluz based on a manuscript name, but Sowerby remains the sole author of this species.

Distribution. The distribution range of *T. macri* cannot be fully elucidated at present (see Remarks). The material studied by Sands et al. (2019a) derives primarily from the drainage systems in eastern Cilicia and nearby drainages in south-east Anatolia (Fig. 3A).

Theodoxus major Issel, 1865

Figure 19A–Zb

Neritina liturata Eichwald 1838: 156–157; Martens 1879: 223–224, pl. 21, figs 24–26; Kobelt 1899: 8, pl. 212, fig. 1336 (**non** *Neritina liturata* Schultze, 1826).

Theodoxus schirazensis var. *major* Issel 1865: 24; Issel 1866: 408.

Neritina Schultzii Grimm 1877: 77–78, pl. 7, fig. 5, pl. 8, fig. 16.

Neritina Schulzii [sic]: Martens 1879: 239–240, pl. 23, figs 13–16.

Theodoxus pallasi Lindholm 1924: 33, 34 (nom. nov. pro *Neritina liturata* Eichwald, 1838, **non** Schultze, 1826); Starobogatov 1974: 255–256, text fig. 224; Akramovskiy 1976: 88, text fig. 23, pl. 1, figs 1, 2; Anistratenko et al. 2017: 221, figs 4, 7, 10, 11; Neubauer et al. 2018: 48–51, figs 4A–F; Wesselingh et al. 2019: 64–65; Glöer 2019: 48–49, fig. 36.

Theodoxus (*Theodoxus*) *pallasi* var. *nalivkini* Kolesnikov 1947: 106, 110.

Theodoxus (*Ninnia*) *schultzi* [sic] var. *jukovi* Kolesnikov 1947: 106, 110.

Theodoxus zhukovi [sic]: Starobogatov 1974: 255, text fig. 223.

Theodoxus astrachanicus Starobogatov in Starobogatov et al. 1994: 8–9, fig. 1(1–2); Degtyarenko and Anistratenko 2013: 22–23, pl. 1, fig. 2a–c.

Theodoxus (*Theodoxus*) *schultzii*: Zettler 2007: 249–250, figs 4a–h, 5a–h; Vinarski and Kantor 2016: 157.

? *Theodoxus doriae*: Mansoorian and Samaee 2012: 44–45 (partim, only material from Gilan and Mazandaran provinces; **non** *Theodoxus doriae* Issel, 1865 [= *T. pallidus*])

Figure 19. *Theodoxus major* Issel, 1865. **A**, **B**. Specimen (*T. pallasi*-morphotype) collected in the Caspian Sea, offshore from Aktau, Kazakhstan (UGSB 20712); **C**, **D**. Specimen (*T. pallasi*-morphotype) collected in the Aral Sea, Kazakhstan in 1979 (UGSB 19129); **E–H**. Specimen (*T. pallasi*-morphotype) from the Shahpol River, Aliabad Askar Khan, Iran (UGSB 18091); **I–K**. Specimen of *T. major* collected at the outflow of Lake Akna, Aknalich, Armenia (UGSB 20482); **L–N**. Specimen (*T. astrachanicus*-morphotype) collected in Utlyukskij Liman, Ukraine (UGSB 18130); **O**, **P**. Specimen of *T. major* collected in the Hrazdan River at the inflow of the Yerevan Reservoir, Armenia (UGSB 20496); **Q–T**. Specimen of *T. major* from Zoeram, North Khorasan, Iran (UGSB 21661); **U**, **V**. Specimen of *T. schultzii* collected in the Caspian Sea, offshore from Aktau, Kazakhstan (UGSB 20714); **W–Y**. Lectotype of *T. pallasi* from Caspian Sea, Dagestan, Russia (ZIN 54547/63); **Za**, **Zb**. Syntype of *N. schultzii* from the Caspian Sea (ZIN, no. 5 in systematic catalogue). Specimens E–K and O–T used in the phylogeny (Fig. 2). Scale bars: 1 mm.

? *Theodoxus euphraticus*: Mansoorian and Samaee 2012: 61 (partim, only material from the Khorasan provinces; **non** *Neritina euphratica* Mousson, 1874 [= *T. jordani*])

Theodoxus fluviatilis: Glöer and Pešić 2012: 16–17 (partim, only Khorrasan material; **non** *Nerita fluviatilis* Linnaeus, 1758).

Theodoxus (*Theodoxus*) *astrachanicus*: Vinarski and Kantor 2016: 155–156.

Theodoxus (*Theodoxus*) *pallasi*: Vinarski and Kantor 2016: 156–157 (and synonyms therein).

Theodoxus schultzii: Wesselingh et al. 2019: 66; Glöer 2019: 52, fig. 40.

Theodoxus major: Sands et al. 2019b: 3, fig. 1.

Type locality. Lake Sevan, Armenia. However, Akramovskiy (1976) suggested the type locality given by Issel (1865) was erroneous and should be Yerevan in Armenia.

Type material. The syntypes of *T. schirazensis* var. *major* are supposed to be stored in MRSN, but the collection is inaccessible at the moment due to renovation and restoration of the museum (E. Gavetti pers. comm. 09/2019). The lectotype of *N. liturata* and *T. pallasi* (designated by Starobogatov et al. 1994) is stored in ZIN (coll. no. 54547/63). Twenty syntypes of *N. schultzii* are stored in ZIN (coll. no. 6214/5) and a single in ZMD (coll. no. ZB-M W. Dyb. 71; see Anistratenko et al. 2018).

Remarks. Wesselingh et al. (2019) reviewed the taxonomy of the Pontocaspian *Theodoxus* spp. They showed that *N. liturata* Eichwald, 1838 (described from Derbent, Dagestan, Russia, north-western Caspian Sea) was invalid as a junior primary homonym of *N. liturata* Schultze, 1826 (described from the Americas) and was replaced by Lindholm (1924) with *T. pallasi* Lindholm, 1924. Moreover, they supported the synonymy of *T. astrachanicus* Starobogatov in Starobogatov et al. 1994 with *T. pallasi* (Anistratenko et al. 2017). Wesselingh et al. (2019) additionally suggested *T. schultzii* (Grimm, 1877) and *T. major* (the latter originally described as a variety of the unavailable name *T. schirazensis*) may additionally be conspecific with *T. pallasi* given morphological similarities. However, Wesselingh et al. (2019) refrained from synonymising *T. major*, *T. pallasi*, and *T. schultzii*, pending molecular support. This was provided recently by Sands et al. (2019b), who corroborated the synonymy of *T. astrachanicus*, *T. major*, *T. schultzii*, and *T. pallasi* (also see Fig. 2). As already argued by Wesselingh et al. (2019), the name *T. major* has priority.

There is large intraspecific morphological variability within this species, especially regarding the radula, shell shape and periostracum colouration (Zettler 2007; Anistratenko et al. 2017; Fig. 19). For example, specimens from deeper parts of the Caspian Sea (*T. schultzii*-morphotype) may lack colouration and have a broadened columellar plate making the shell look somewhat flattened (Zettler 2007; Fig. 19), while shoreline samples (*T. pallasi*-morphotype) lack this broadened columellar plate and display clear, black diagonal banding patterning (Fig. 19). Inland specimens (*T. major*-morphotype) from Iran and Armenia tend to be dark and with a less distinct banding pattern (Fig. 19). The operculum of this species is somewhat similar to those of *T. pallidus*, *T. fluviatilis*, and *T. velox* with a strong rib-shield and no pseudo-apophysis (Figs 9, 10, 19, 20, 22). It is not surprising that molecular data of material from locations in Khorrasan province studied by Glöer and Pešić (2012) and identified as *T. fluviatilis* conforms to *T. major* (Sands et al. 2019b; Fig. 2). Akramovskiy (1971) already suggested that specimens considered *T. subthermalis* [= *T. fluviatilis*] from Armenia represented black-coloured morphotypes of *T. pallasi* [= *T. major*]. However, *T. major* only shares a close phylogenetic relationship with *T. pallidus* and likely diverged from their common ancestor during the Pleistocene (Sands et al. 2019b; Fig. 2).

Distribution. *Theodoxus major* is found in the Caspian Sea and parts of the Azov Sea (Roth 1987, Karpinsky 2002; Anistratenko et al. 2017; Sands et al. 2019a) and is also present in the Volga and Don river systems (Sands et al. 2019b). It has likely become regionally extinct in the Aral Sea (Andreev et al. 1992; Aladin et al. 1998; Plotnikov et al. 2016), although it may still persist in some of its associated drainages (Zettler 2007). In Western Asia it can be found in the Aras River system (Aliyev and Ahmadi 2010), Lake Yerevan and its catchment systems in Armenia (Sands et al. 2019b), and Masalli in Azerbaijan. Records of *T. doriae* Issel, 1865 [= *T. pallidus*], *T. euphraticus* [= *T. jordani*], or *T. fluviatilis* by Glöer and Pešić (2012) and Mansoorian and Samaee (2012) from several mineral springs and streams in Gilan, Mazandaran, and the Khorasan provinces of northern Iran are likely misidentifications of *T. major* (Sands et al. 2019b; Fig. 3B). Its presence in Lake Sevan (the supposed type locality) or the adjacent area around the lake was questioned by Akramovskiy (1976) (see above).

Theodoxus pallidus (Dunker, 1861)

Figure 20A–Y

Neritina pallida Dunker 1861: 40; Martens 1879: 239, pl. 23, figs 11, 12; Kobelt 1899: 13, pl. 214, fig. 1349.

Theodoxus Doriae Issel 1865: 23–24; Issel 1866: 407–408; Biggs 1937: 349; Mansoorian and Samaee 2012: 55–56 (partim, only material from Chaharmahal and Bakhtiari, Isfahan, and Yazd provinces).

Neritina Doriae: Martens 1879: 222–223, pl. 21, figs 22, 23; Kobelt 1899: 7–8, pl. 212, fig. 1335.

Theodoxus doriae var. *obscura* Biggs 1937: 349.

Theodoxus pallidus: Starmühlner and Edlauer 1957: 437–442, text figs 1–5, fig. 1a (synonymy tentative); Roth 1987: 75; Sands et al. 2019b: 3, fig. 1.

? *Theodoxus* (*Theodoxus*) *doriae*: Schütt and Şeşen 1989b: 41.

? *Theodoxus euphraticus*: Mansoorian and Samaee 2012: 56–59 (partim, only material from Kerman and Yazd provinces; **non** *Neritina euphratica* Mousson, 1874 [= *T. jordani*])

Theodoxus fluviatilis: Glöer and Pešić 2012: 16–17 (partim, only Fars and Hormozgan material; **non** *Nerita fluviatilis* Linnaeus, 1758).

Theodoxus pallida [sic]: Glöer and Pešić 2012: 17–18, fig. 3a–c.

Type locality. Southern Persia (= Iran).

Type material. Two syntypes of *N. pallida* are deposited in ZMB (coll. no. ZMB/Moll 108792-108793). Nine

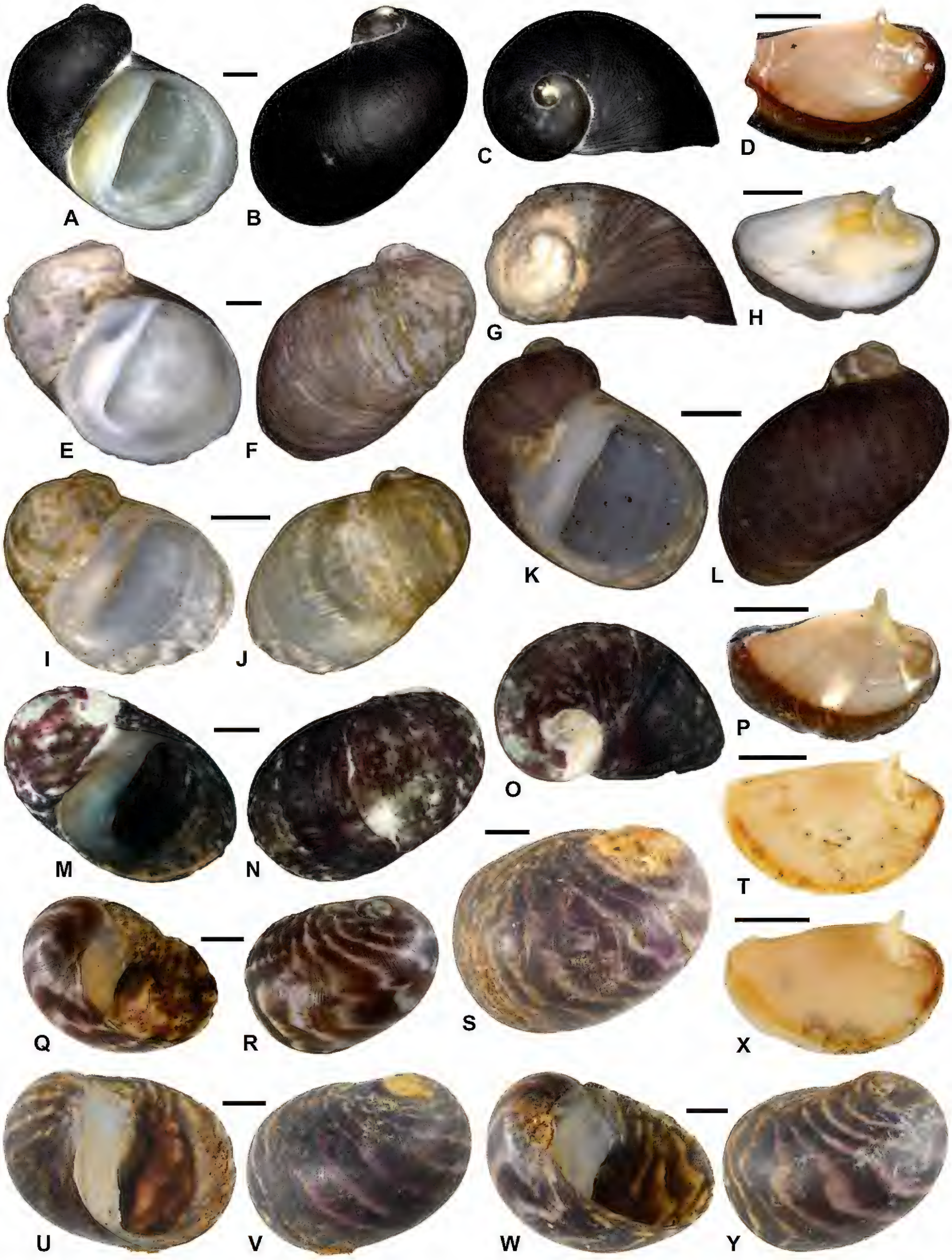

Figure 20. *Theodoxus pallidus* (Dunker, 1861). **A–D**. Specimen from Haji Abad, Fars, Iran (UGSB 22227); **E–H**. Syntype of *N. pallida* from southern Iran (ZMB 108.792); **I**, **J**; **K**, **L**. Two syntypes of *N. pallida* from southern Iran (ZMB 108.793); **M–P**. Specimen (*T. doriae*-morphotype) from a spring near Harat, Yazd, Iran (UGSB 21706); **Q**, **R**; **S**, **T**; **U**, **V**; **W–Y**. Four syntypes of *N. doriae* from the thermal springs of Kerman, Iran (MSNG, without coll. no.). Specimens A–D and M–P were used in the phylogeny. Scale bars: 1 mm.

syntypes of *N. doriae* are stored in MSNG (without coll. no.). The holotype of *T. doriae* var. *obscura* from Aqda, Iran, is stored in BMNH (coll. no. 1958.6.13.22).

Remarks. *Theodoxus pallidus* was described by Dunker (1861) from southern Persia (present-day Iran). Starmühlner and Edlauer (1957) synonymised *T. pallidus* and *T. doriae* based on similarities among the material and distinguished this species from *T. fluviatilis* by a higher spire (Figs 9, 10, 20). Glöer and Pešić (2012) recently reviewed the material of *T. pallidus* from Starmühlner and Edlauer (1957) and corroborated the differentiation from *T. fluviatilis* and provided more differentiating features based on the operculum. However, Glöer and Pešić (2012) differed in the synonymy of *T. doriae*, which they synonymised with *T. fluviatilis*. Molecular data of material from southern Iran conforming to Dunker's (1861) description of *T. pallidus* and material of *T. doriae* from Kerman province support the independence of *T. pallidus* from *T. fluviatilis*, as well as the synonymy of *T. pallidus* and *T. doriae* as suggested by Starmühlner and Edlauer (1957) (Sands et al. 2019b). In turn, *T. pallidus* shares a close sister-species relationship with *T. major* (Sands et al. 2019b; Fig. 2). The pronouncement of the spire seems to vary among populations in *T. pallidus* and the shell shape may largely mimic those seen in *T. major* (except *T. schultzii*-morphotype). However, this species seems to be dominated by black morphs or specimens with thicker dark banding, and the conchioline lamella is much more reduced in comparison to the sister species (Figs 19, 20).

Theodoxus doriae var. *obscura* Biggs, 1937 ranges within the variability shown by the syntype series of *T. doriae* (Fig. 20Q–Y) concerning shell shape and colouration and is consequently considered a junior synonym of *T. pallidus*.

Distribution. All records of *T. pallidus* are restricted to south-central Persia and occur from the Zagros Mountains eastward in at least Chaharmahal and Bakhtiari, Fars, Hormozgan, Isfahan, Kerman, and Yazd provinces of Iran (Starmühlner and Edlauer 1957; Mansoorian and Samaee 2012; Sands et al. 2019b; Fig. 3B). Records of *T. doriae* [= *T. pallidus*] from Gilan and Mazandaran provinces by Mansoorian and Samaee (2012) and North Khorasan and Razavi Khorasan provinces by Glöer and Pešić (2012) are likely misidentified *T. major* (Sands et al. 2019b; Fig. 3B), and those from Anatolia (Roth 1987) are likely misidentified *T. fluviatilis* (Sands et al. 2019a).

Theodoxus syriacus (Bourguignat, 1852)

Figure 21A–R

Neritina Syriaca Bourguignat 1852: 26; Martens 1874: 33, pl. 5, fig. 41; Martens 1879: 238, pl. 23, figs 9, 10; Kobelt 1899: 12–13, pl. 214, fig. 1348.

Theodoxus (*Theodoxus*) *syriacus*: Schütt and Seşen 1989b: 40–41.

Theodoxus syriacus: Yıldırım 1999: 885; Gürlek et al. 2019: 2993; Glöer 2019: 53, fig. 42.

Type locality. Beirut, Lebanon.

Type material. The syntype series is supposed to be stored in MHNG but could not be found (E. Tardy pers. comm. 11/2018). The only material collected by Bourguignat available there was collected from İskenderun, Turkey (coll. no. MHNG-MOLL-111712).

Remarks. Bourguignat (1852) described *T. syriacus* from Beirut, Lebanon, which lacked a pseudo-apophysis. Martens (1874) lacked Bourguignat's material, but he connected the name and diagnostic features to specimens from Kahramanmaraş, Turkey. Nothing conforming to *T. syriacus* has been found around Beirut in recent times (van Damme 2014). However, Schütt and Şeşen (1989b), Yıldırım et al. (2006), and Gürlek et al. (2019) reported this species from a number of localities in south-east Anatolia. Sands et al. (2019a) sequenced specimens of *Theodoxus* from these localities and noted that the material that conformed to *T. syriacus* formed a distinct clade (also see Fig. 2). Interestingly, they also found that a specimen from Greece attributed to *T. peloponensis* (Récluz, 1841) by Bunje and Lindberg (2007) was genetically linked to this species (Sands et al. 2019a). Given the earlier description of *T. peloponensis*, that name would take precedence. However, the morphological conformity of this specimen to the type material of *T. peloponensis* could not be confirmed. Given the disjunct geographic distribution range this may be a case of a misplaced or mislabelled sample, and we encourage future review of this species.

Besides the lack of a pseudo-apophysis, *T. syriacus* operculum has a reduced rib-shield and an ivory calcareous base (Fig. 21D, H, L). The shells are often uniform black or dark brown and less globular (elongated width), but occasionally speckled forms with ivory patches can be found (Fig. 21A–R). *Theodoxus syriacus* shares close relationships with both *T. wesselinghi* sp. nov. and *T. wilkei* sp. nov. (Sands et al. 2019a; Fig. 2). These species likely diverged from a common ancestor around the Pliocene–Pleistocene transition (Sands et al. 2019a; Fig. 2).

Distribution. South-eastern Anatolia and north-western Mesopotamia, particularly in Adana, Diyarbakır, Elazığ, Kahraman Maraş, Malatya, Mardin, and Tunceli provinces of Turkey (Schütt and Şeşen 1989b; Yıldırım 1999; Yıldırım et al. 2006; Gürlek et al. 2019; Sands et al. 2019a; Fig. 3D). Possibly regionally extinct or very localised in Lebanon and Syria (van Damme 2014). Records from Greece are questionable and need confirmation.

Theodoxus velox V. Anistratenko in O. Anistratenko et al., 1999

Figure 22A–M

Theodoxus velox V. Anistratenko in O. Anistratenko et al. 1999: 17–18, fig. 4.7; Wesselingh et al. 2019: 66.

Type locality. Dnieper Delta, Zburievkiy Liman, Kherson Region, Ukraine.

Type material. Holotype and five paratypes are stored in IZAN (without coll. no.).

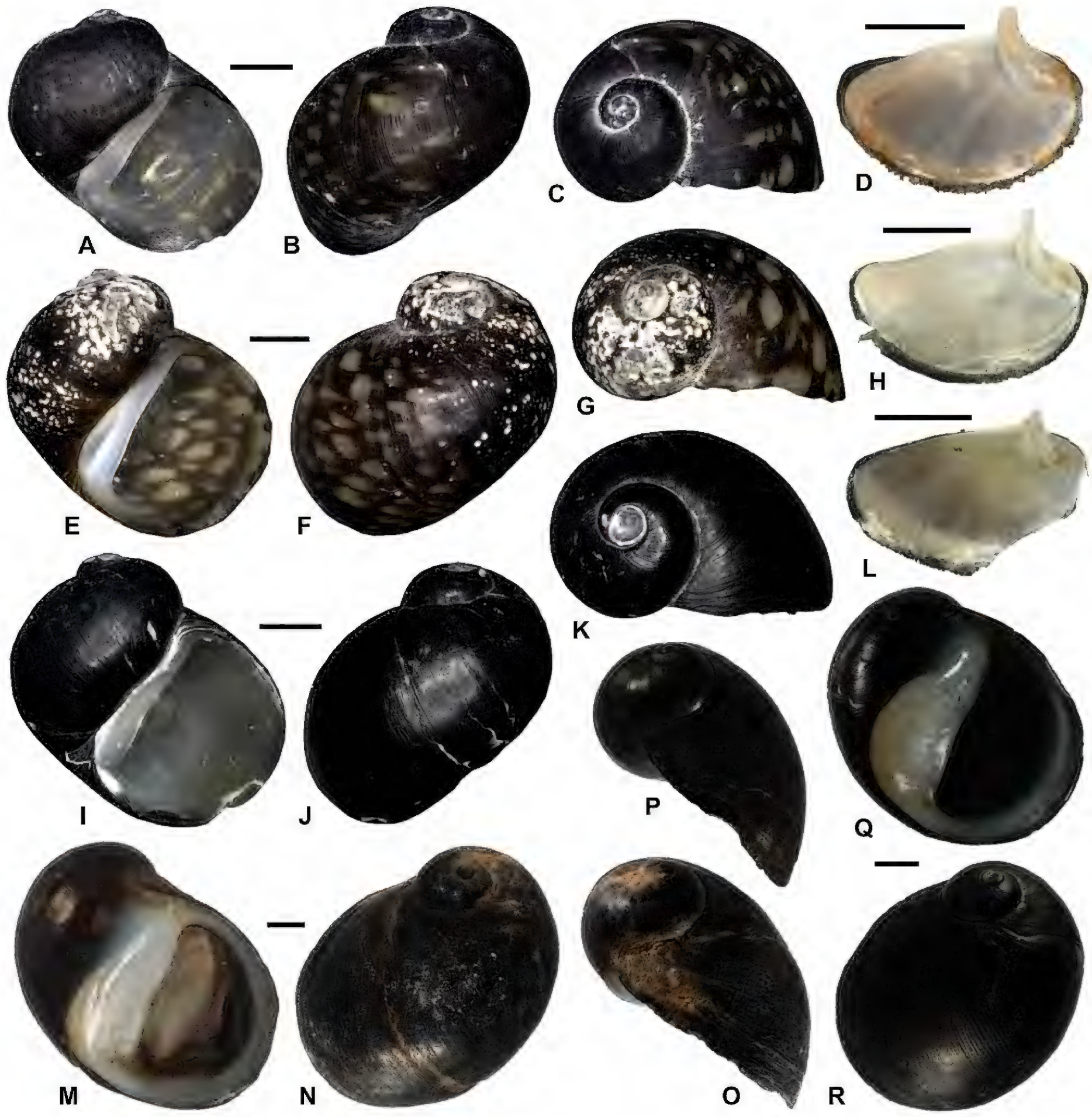

Figure 21. *Theodoxus syriacus* (Bourguignat, 1852). **A–D**. Specimen collected at Sultanköyü, Mardin, Turkey (UGSB 24182); **E–H**. Specimen from the Yanarsu Stream, Alıçlı, Turkey (UGSB 20518). **I–L**. Specimen collected near Başdeğirmen, Diyarbakır, Turkey (UGSB 24183); **M–O**; **P–R**. Two specimens collected by Bourguignat from İskenderun, Turkey (MHNG-MOLL-111712). All UGSB specimens incorporated into the phylogeny (Fig. 2). Scale bars: 1 mm.

Remarks. This species was recently discussed by Wesselingh et al. (2019). While it was previously considered a junior synonym of *T. fluviatilis* (Vinarski and Kantor 2016), molecular data shows strong monophyletic support for the independence of *T. velox* (Sands et al. 2019a; Fig. 2). Nevertheless, *T. velox* and *T. fluviatilis* still hold a sister relationship and likely diverged from one another during the early Pleistocene (Sands et al. 2019a; Fig. 2). *Theodoxus velox* is challenging to distinguish from *T. fluviatilis* given the overlap in geographic range and similarity of conchological features (Figs 3, 9, 10, 22). *Theodoxus velox* has less phenotypic variability compared to *T. fluviatilis* (Figs 9, 10, 22). Moreover, *T. velox* display more expansive spiral whorls and, in some instances, a more transparent operculum where the conchioline lamella extends deeper into the calcareous base and the callus is less pronounced (Figs 9, 10, 22).

The geographic distribution range of *T. velox* overlaps with that of *T. sarmaticus* (Lindholm, 1901), which has been considered a junior synonym of *T. fluviatilis* (e.g. Vinarski and Kantor 2016). While *T.*

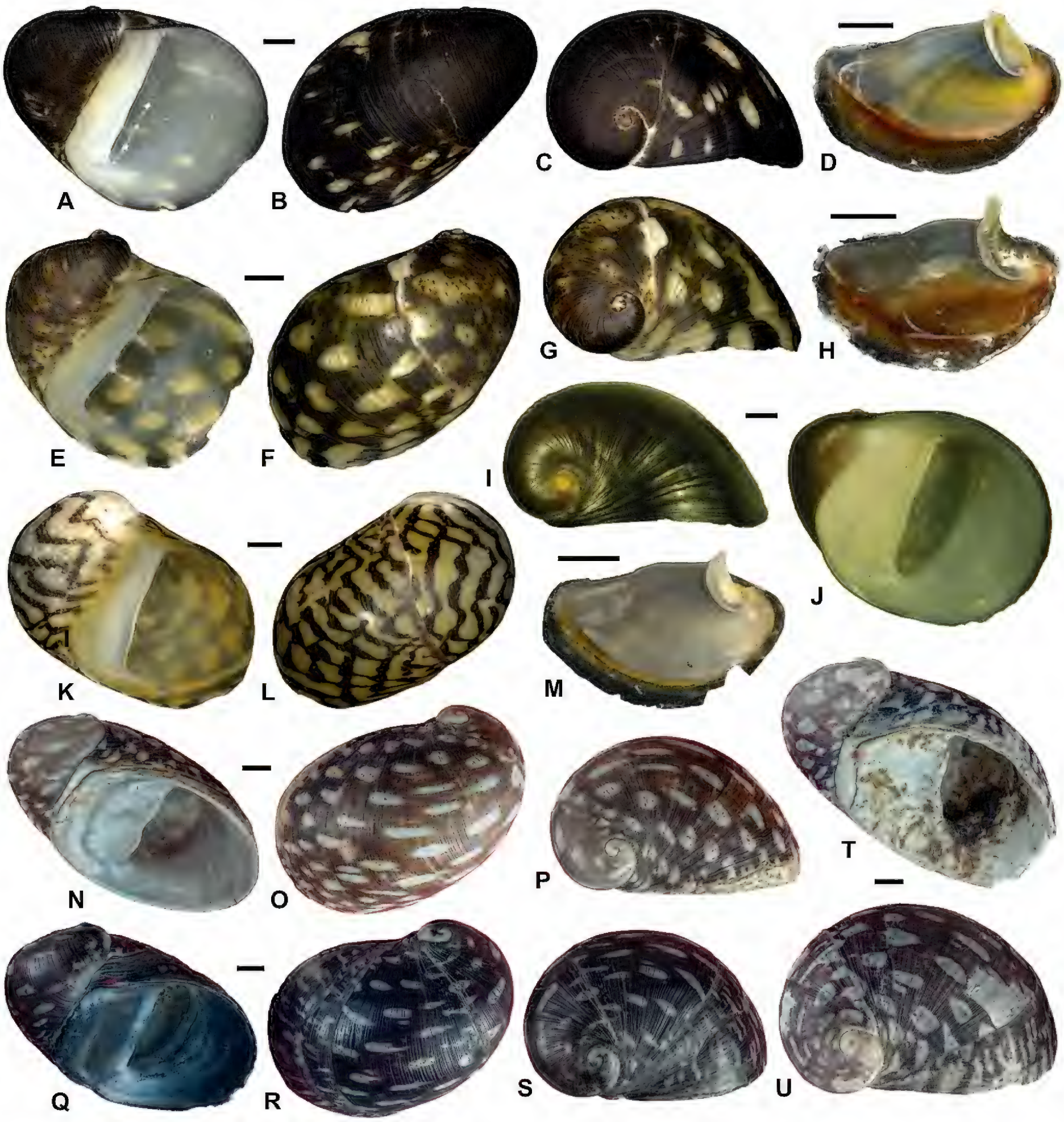

Figure 22. *Theodoxus velox* V. Anistratenko in O. Anistratenko et al., 1999. **A–D**. Specimen from the Dnieper River, Kiev, Ukraine (UGSB 24186); **E–H**. Specimen collected in the Danube delta, Vylkove, Ukraine (UGSB 24184) used in the phylogeny (Fig. 2); **I**, **J**. Holotype from Dnieper Delta, Zbur'ivka Liman, Ukraine (IZAN); **K–M**. Specimen from Lake Sapanca, Yeni Eşme, Turkey (UGSB 20691). *Theodoxus sarmaticus* (Lindholm, 1901). **N–P**; **Q–S**; **T–U**. Three syntypes from the Oskol River, near Golubino, Russia stored in ZIN (coll. no. 6099/24). Scale bars: 1 mm.

sarmaticus and *T. fluviatilis* may on occasion share phenotypic similarity, the morphotypes of *T. sarmaticus* closely resemble *T. velox* (Fig. 22A–M versus Fig. 22N–U). The similarity with *T. velox* could suggest *T. sarmaticus* is rather conspecific with that species as suggested by Glöer (2019). Unfortunately, no opercula or soft tissues were preserved among the syntypes of *T. sarmaticus* to corroborate this hypothesis. Molecular analyses of topotypic material is required to address this uncertainty. However, should this be confirmed at a later point, the name *T. sarmaticus* would have priority.

Distribution. This species was indicated to be restricted to drainage systems of the northern Black Sea coast (Anistratenko et al. 1999; Kantor and Sysoev 2006). Recent molecular data suggest it is distributed as far North as the eastern part of the Baltic Sea and as far South as Anatolia (Sands et al. 2019a): the only record there derives from Lake Sapanca (Sands et al. 2019a; Fig. 3C).

Figure 23. Type locality of *Theodoxus wesselinghi* Sands & Glöer sp. nov. **A**, **B**. Sakarya River, Çayköy, Bilecik, Turkey, 40.0439°N, 30.452°E. Further paratype localities: **C**, **D**. Unnamed roadside spring in Fele, Isparta province, Turkey, 38.00358°N, 31.47217°E; **E**, **F**. Eflatun Pınarı, near Sadıkhacı, Konya, Turkey, 37.8256°N, 31.6748°E; **G**, **H**. Balıkdamı Wetland spring, Eskişehir, Turkey, 39.15277°N, 31.61562°E.

Theodoxus wesselinghi Sands & Glöer, sp. nov.

http://zoobank.org/97AF034D-EF6D-4AB2-AC17-0C5B037C8DAD

Figures 23A–H, 24A–M, 25A–F

Theodoxus fluviatilis: Odabaşı and Arslan 2015: 330–331 (**non** *Nerita fluviatilis* Linnaeus, 1758).

Theodoxus anatolicus: Yıldırım et al. 2018: 118 (**non** *Nerita anatolica* Récluz, 1841).

Type locality. Sakarya River, Çayköy, Bilecik, Turkey; 40.0439°N, 30.452°E (Figs 3D, 23A, B).

Holotype. RMNH.MOL.342200 (Sakarya River, Çayköy, Bilecik, Turkey; 40.0439°N, 30.452°E) stored in NMNL: Shell height 6.0 mm, width 6.0 mm (Fig. 24A–D).

Paratypes. Twenty-four specimens from Sakarya River, Çayköy, Bilecik, Turkey; 40.0439°N, 30.452°E (Fig. 23A, B): 11 in NMNL (RMNH.MOL.342201,

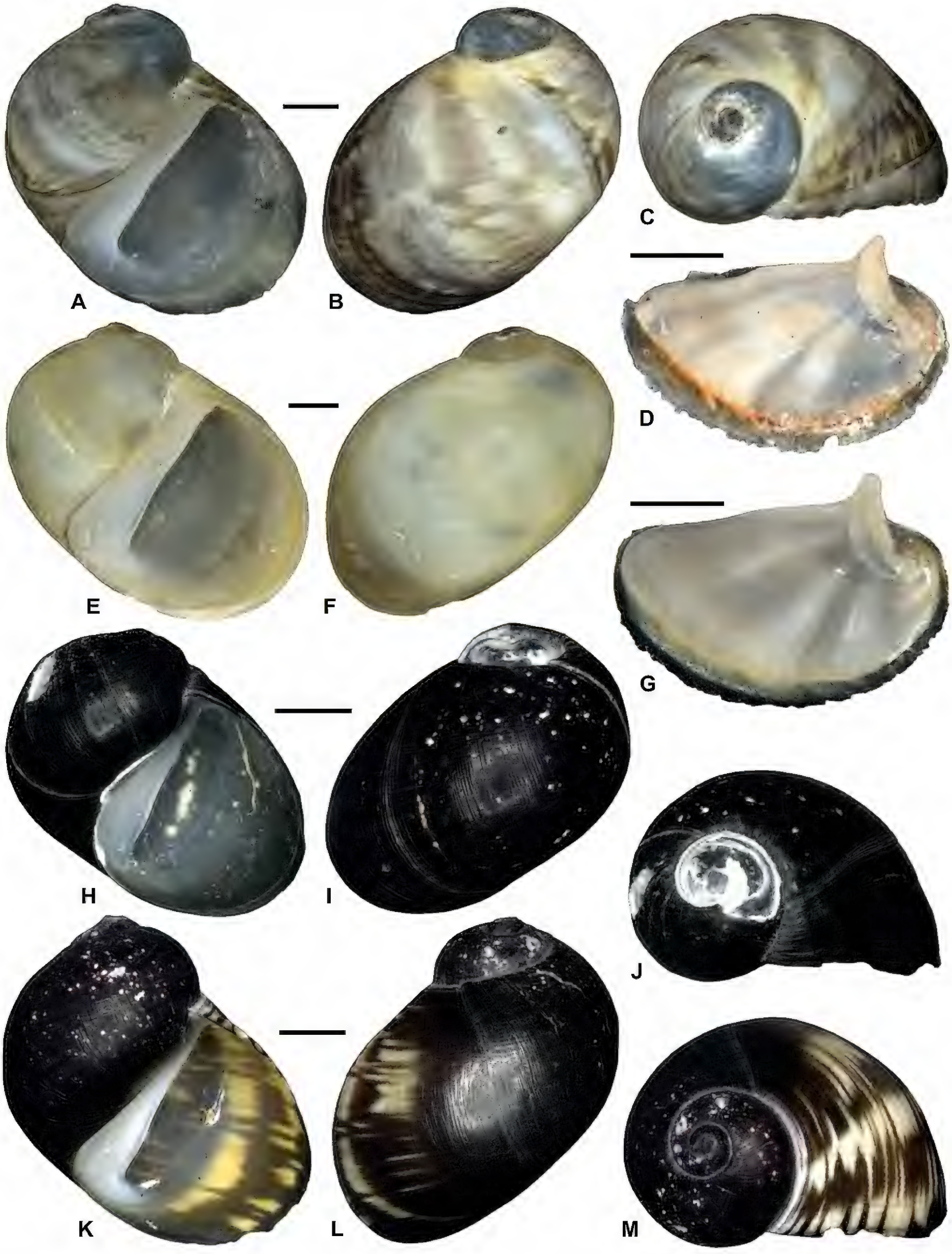

Figure 24. *Theodoxus wesselinghi* Sands & Glöer sp. nov. **A–D**. Holotype collected in the Sakarya River, Çayköy, Bilecik, Turkey (RMNH.MOL.342200); **E–G**. Paratype from the same location as the holotype (RMNH.MOL.342202); **H–J**. Paratype from Fele, Isparta province, Turkey (RMNH.MOL.342204); **K–M**. Paratype from Eflatun Pınarı, Konya province, Turkey (RMNH.MOL.342206). All photographed material (A–M) is stored in NMNL. Scale bars: 1 mm.

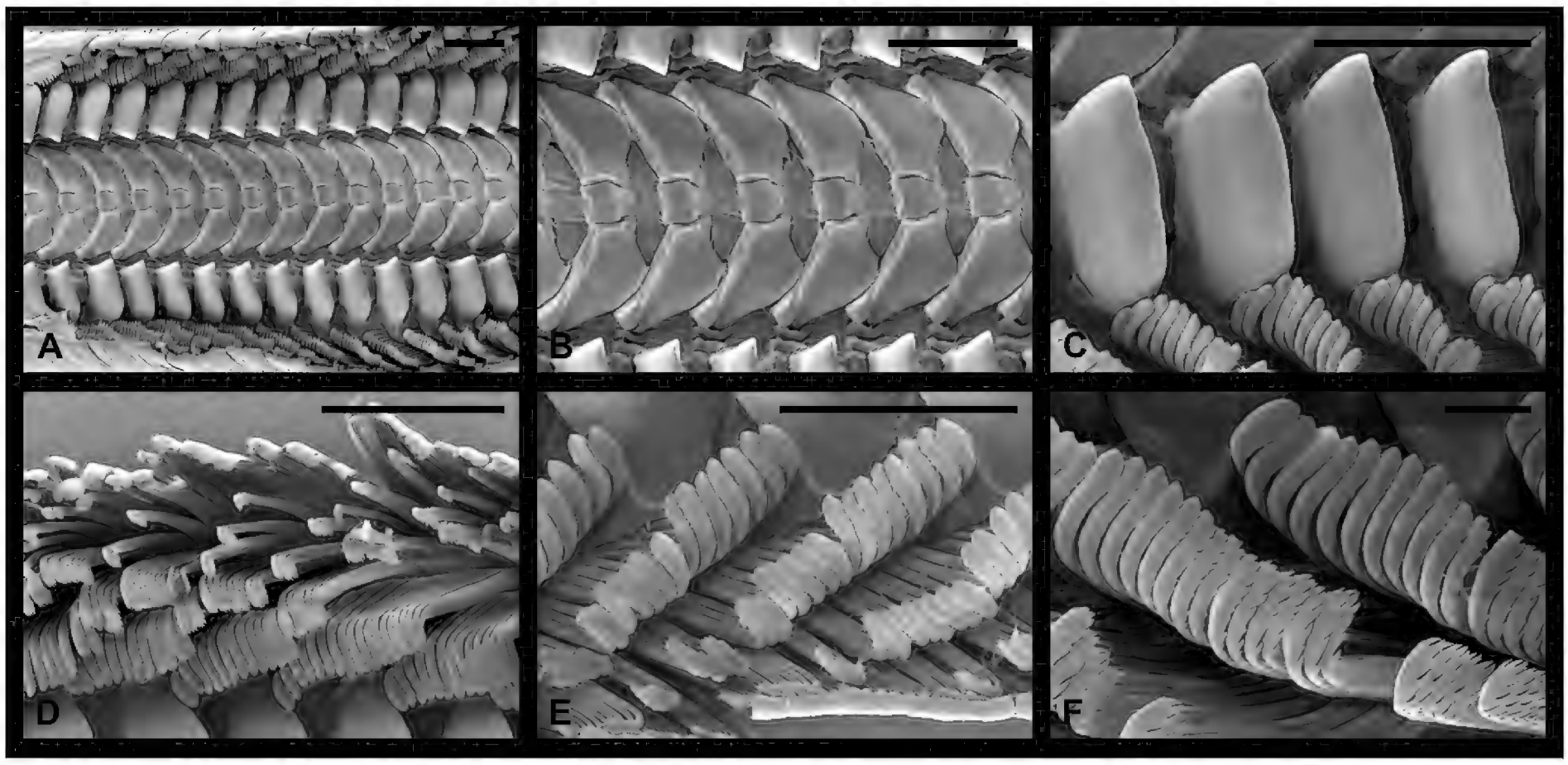

Figure 25. Radula of *Theodoxus wesselinghi* Sands & Glöer sp. nov. paratypes. **A**. Portion of the radula showing full sets of teeth (UGSB 20688); **B**. Magnified view of the central teeth (UGSB 20688); **C**. Magnified view of the lateral and marginal teeth (UGSB 20686); **D**. Magnified view of the first and second rows of marginal teeth (UGSB 20688); **E**. Magnified view of the first row of marginal teeth (UGSB 20686); **F**. Magnified view of the faces of inner marginal teeth belonging to the first row (UGSB 20685). Scale bars: 100 μm (A–E), 20 μm (F).

RMNH.MOL.342202; Fig. 24E–G) and 13 in UGSB (UGSB 20688, UGSB 20743, UGSB 20744; Fig. 25A, B, D). Twenty-four specimens from an unnamed roadside spring in Fele, İsparta province, Turkey; 38.00358°N, 31.47217°E (Fig. 23C, D): 11 in NMNL (RMNH.MOL.342203, RMNH.MOL.342204; Fig. 24H–J) and 13 in UGSB (UGSB 20684, UGSB 20735, UGSB 20736). Twenty-five specimens from Eflatun Pınarı, near Sadıkhacı, Konya, Turkey; 37.8256°N, 31.6748°E (Fig. 23E, F): 11 in NMNL (RMNH.MOL.342205, RMNH.MOL.342206; Fig. 24K–M) and 14 in UGSB (UGSB 20685, UGSB 20737, UGSB 20738; Fig. 25F). Thirty specimens from Balıkdamı Wetland spring, Eskişehir, Turkey; 39.15277°N, 31.61562°E (Fig. 23G, H): 13 in NMNL (RMNH.MOL.342207) and 17 in UGSB (UGSB 20686, UGSB 20739, UGSB 20740; Fig. 25C, E).

Etymology. The species is named in honour of the molluscan palaeontologist Frank P. Wesselingh (Naturalis Biodiversity Center, Leiden, The Netherlands) for his contributions to malacology.

Description. Shell (Fig. 24A–C, E, F, H–M): Hemispherical, transversely elongate, consisting of typically three whorls that rapidly grow. Spire well defined, moderate height for *Theodoxus*; often corroded along with other parts of shell. Shell height ranges from 4.0–6.8 mm, width from 3.8–7.1 mm. Juveniles appear more globular. Periostracum is uniformly ivory or solid black, intermediate forms with broad brown-black smudged diagonal stripes also exist; surface glossy, finely striated with growth lines. Aperture semicircular, no serrations on inner lip. Columellar plate smooth, flat to slightly concave, inclined towards aperture; colouration blue-grey in darker shelled individuals to white in lighter forms.

Operculum (Fig. 24D, G): Operculum plate made of two parts, calcareous base and conchioline lamella; operculum base light, mostly ivory to white, white lamella with distinct orange edge on border with operculum base. Operculum base left adductor can be blunt and rounded, weak callus on top right edge. Apophysis follows same colour scheme as operculum calcareous base, broader at top and narrower and attenuated at bottom. Very narrow rib-shield, deep rib-pouch present on operculum. Operculum lacks a pseudo-apophysis.

Radula (Fig. 25A–F): R-central tooth flanked by A-central, B-central, C-central, E-lateral on each side. Additionally, two interconnected layers of marginal teeth encase central and lateral teeth. R-central shows some variation among populations, slightly spherical or more squared face with slightly concave anterior edge. A-central large and flat with thin ridge that becomes broad and folded right at end of cusp. B-central diminished, forms irregular "S" shape. C-central equally diminished, hidden below lower edge of E-lateral. E-lateral simple with smooth upper edge. First layer of marginal teeth consists of 37–44 teeth that decrease in size away from E-lateral but increase in size and bear serrations on edges of small faces; semidetached from second layer, which is fused and forms outer wall.

Differentiating features. Based on conchological features of periostracum colouration and patterning and shell shape, it is difficult to differentiate *T. wesselinghi* sp. nov. from most Asian *Theodoxus* spp. given the variety in colour and patterns among the type material (Fig. 24A–M).

However, in some instances it can be distinguished from Anatolian morphotypes of *T. baeticus*, which typically displays ivory blotches on a brown background (Fig. 7A–D); *T. altenai* with clear ivory checks on a dark brown-black background (Fig. 4A–G) and *T. gloeri* lacking shell pigmentation and bearing strong axial ribs on the shell (Fig. 11A–C). The light ivory-coloured operculum calcareous base makes this species distinct from *T. gurur* sp. nov. (light to dark brown; Figs 13D, 24D, G) and *T. wilkei* sp. nov. (bright orange; Figs 24D, G, 27D).

More differentiating features occur in the operculum structure (Fig. 24D, G). The presence of an attenuated apophysis distinguishes *T. wesselinghi* sp. nov. from *T. altenai* and *T. jordani*, which have non-attenuated apophyses (Figs 4, 15, 17). A rib-pouch and rib-shield are either totally lacking or extremely diminished in *T. altenai*, *T. anatolicus*, *T. jordani*, and *T. macri* (Figs 4, 5, 15, 17, 18), while they are more pronounced in *T. wesselinghi* sp. nov. (Fig. 24). The rib-shield in *T. wesselinghi* sp. nov. is however less broad than that typically observed in *T. fluviatilis* and *T. baeticus* (Figs 6–10). Furthermore, the lack of a pseudo-apophysis differentiates the new species from *T. altenai*, *T. anatolicus*, *T. baeticus*, *T. gurur* sp. nov., *T. jordani*, and *T. macri* (Figs 4–8, 13, 15, 17, 18). Additionally, the presence of a weak callus on the top right edge of the operculum base in *T. wesselinghi* sp. nov. helps to differentiate this species from *T. gurur* sp. nov. and *T. jordani*, which lack a callus (Figs 13, 15, 17, 18, 24), as well as from *T. anatolicus*, *T. fluviatilis*, *T. major*, *T. pallidus*, and *T. wilkei* sp. nov., which have stronger calluses (Figs 5, 9, 10, 19, 20, 24, 27).

Based on the available data for *Theodoxus* ralulae, *T. wesselinghi* sp. nov. can be distinguished by a more globular R-central face from *T. gurur* sp. nov., *T. wilkei* sp. nov., *T. fluviatilis*, and *T. jordani*, where it is more rectangular or triangulate (see Baker 1923; Zettler 2008; Figs 14B, 25B, 28B). Furthermore, the smooth upper edge of the E-lateral can be used to distinguish this species from *T. wilkei* sp. nov. and *T. major*, which generally have E-laterals with serrated edges (see Anistratenko et al. 2017; Figs 25C, 28C, D).

Remarks. *Theodoxus wesselinghi* sp. nov. forms part of a larger clade that includes *T. syriacus* and *T. wilkei* sp. nov., where it shares a closer sister-species relationship with *T. wilkei* sp. nov. (Sands et al. 2019a; Fig. 2). The three species likely diverged from one another in quick succession over the Pliocene–Pleistocene transition (Fig. 2).

Distribution. Known so far only from the four localities in central-west Anatolia (Figs 3D, 23A–H).

Ecology. *Theodoxus wesselinghi* sp. nov. can be found in both springs (Balıkdamı Wetland, Eflatun Pınarı, Fele; Fig. 23C–H) and streams (Sakarya River, Çayköy; Fig. 23A, B) with clear water. The occurrence of macrophytes appears negligible to the species as it occurs in localities both with (Fig. 23E–H) and without (Fig. 23A–D) aquatic plant growth. The floors of all localities are made up of coarse grained sand and large and small rocks and stones that *T. wesselinghi* sp. nov. is often attached to (personal observation M.E.G.; Fig. 23H). *Theodoxus wesselinghi* sp. nov. co-occurs with *Potamopyrgus antipodarum* (Gray, 1843) and *Isparta felei* Yıldırım, Koca, Gürlek & Glöer, 2018 in Fele spring, *Falsipyrgula* sp. in Eflatun Pınarı, and *Pseudamnicola natolica* (Küster, 1852) (and possibly also *T. gloeri*; Odabaşı and Arslan 2015) in the Balıkdamı Wetland spring (personal observation M.E.G.).

Theodoxus wilkei Sands & Glöer. sp. nov.

http://zoobank.org/EE48E51C-4D74-4A75-BB9A-F4DECE9A2AEB

Figures 26A, B, 27A–J, 28A–F

Type locality. Çifteler spring, Çifteler, Eskişehir, Turkey; 39.34931°N, 31.05527°E (Figs 3D, 26A, B).

Holotype. RMNH.MOL.342208 (Çifteler spring, Çifteler, Eskişehir, Turkey; 39.34931°N, 31.05527°E) stored in NMNL: Shell height 6.9 mm, width 7.5 mm (Fig. 28A–D).

Paratypes. Nineteen specimens from Çifteler spring, Çifteler, Eskişehir, Turkey; 39.34931°N, 31.05527°E (Fig. 26A, B): 10 in NMNL (RMNH.MOL.342209–342211; Fig. 27E–J) and 9 in UGSB (UGSB 20687, UGSB 20741, UGSB 20742; Fig. 28A–F).

Etymology. The species is named after the molluscan phylogeneticist and evolutionary biologist Thomas Wilke (Justus Liebig University Giessen, Germany).

Description. Shell (Fig. 27A–C, E–J): Hemispherical, transversely slightly elongate, consisting of typically three whorls that rapidly grow. Spire low, apex often corroded. Shell height ranges from 4.5–7.8 mm, width from 5.2–8.6 mm. Periostracum colour and patterning uniformly ivory or black, intermediate forms black with white-ivory speckles or stripes also exist; surface glossy or dull but always finely striated with growth lines. Aperture semicircular with no serrations on inner lip. Columellar plate is smooth, flat to slightly concave, inclined towards aperture; blue-grey in colour, some yellowing around edges.

Operculum (Fig. 27D): Operculum plate made of two parts, calcareous base and conchioline lamella; operculum base bright yellow to deep orange, darkened orange-brown lamella. Left adductor on operculum base blunt and rounded. Strongly defined callus at top right edge of operculum base. Apophysis light to bright yellow. Apophysis broader at top, narrower at bottom (attenuated). Narrow rib-shield and small rib-pouch present on operculum; pseudo-apophysis lacking.

Radula (Fig. 28A–F): R-central tooth flanked by A-central, B-central, C-central, E-lateral of each side. Additionally, two interconnected layers of marginal teeth encase central and lateral teeth. R-central varies in face shape; can be square face with slightly concave anterior edge or more triangular. A-central large and flat with strong

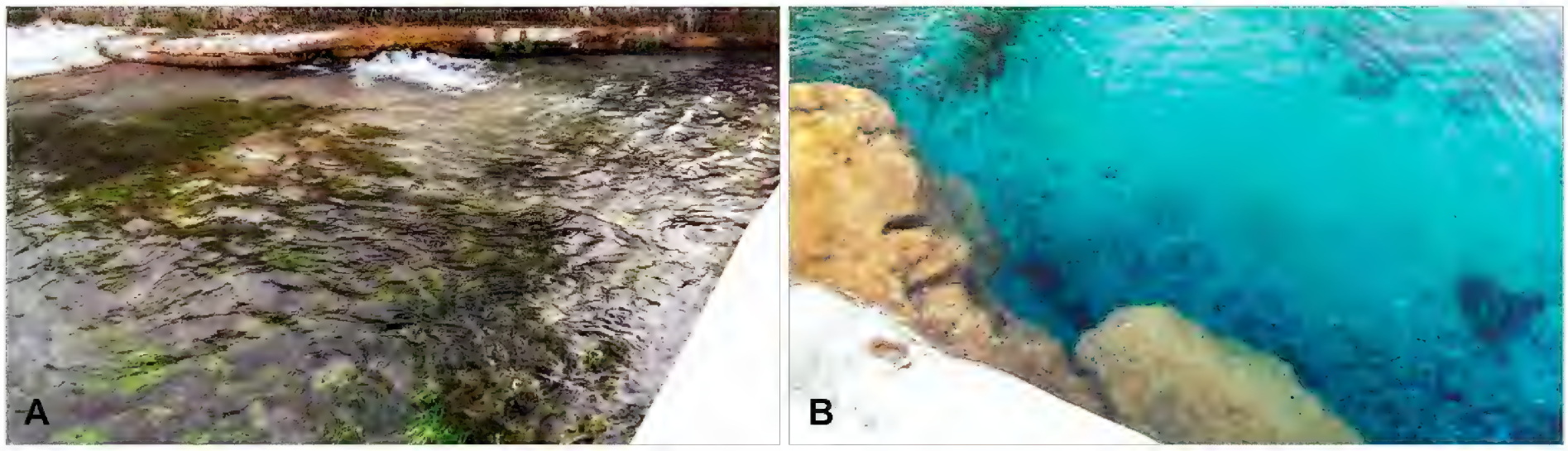

Figure 26. Type locality of *Theodoxus wilkei* Sands & Glöer sp. nov. **A**, **B**. Çifteler spring, Çifteler, Eskişehir, Turkey, 39.34931°N, 31.05527°E.

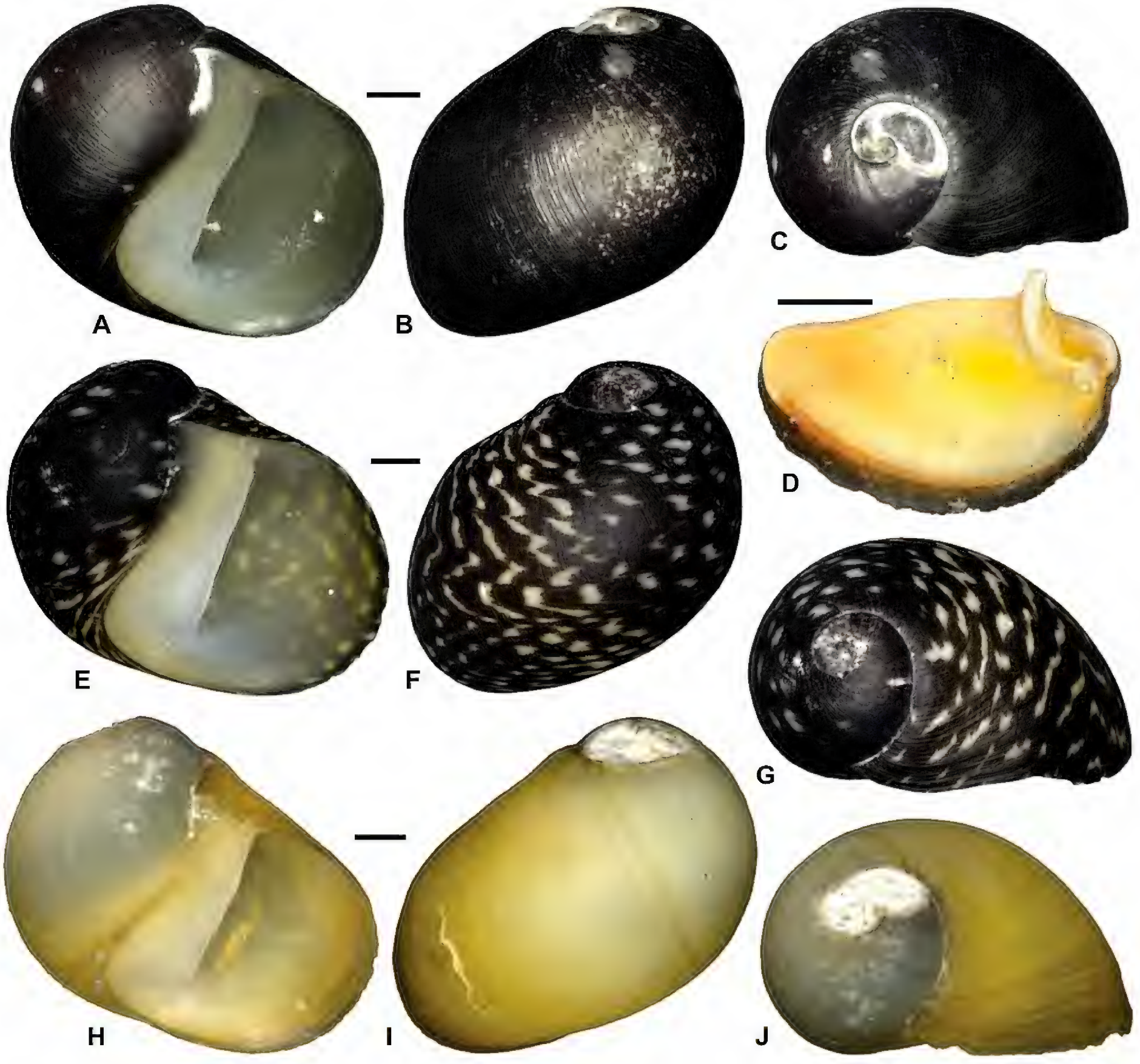

Figure 27. *Theodoxus wilkei* Sands & Glöer sp. nov. **A–D**. Holotype (RMNH.MOL.342208); **E–G**. Paratype (RMNH.MOL.342210); **H–J**. Paratype (RMNH.MOL.342211). All photographed material is from the Çifteler Spring, Çifteler, Eskişehir, Turkey and stored in NMNL. Scale bars: 1 mm.

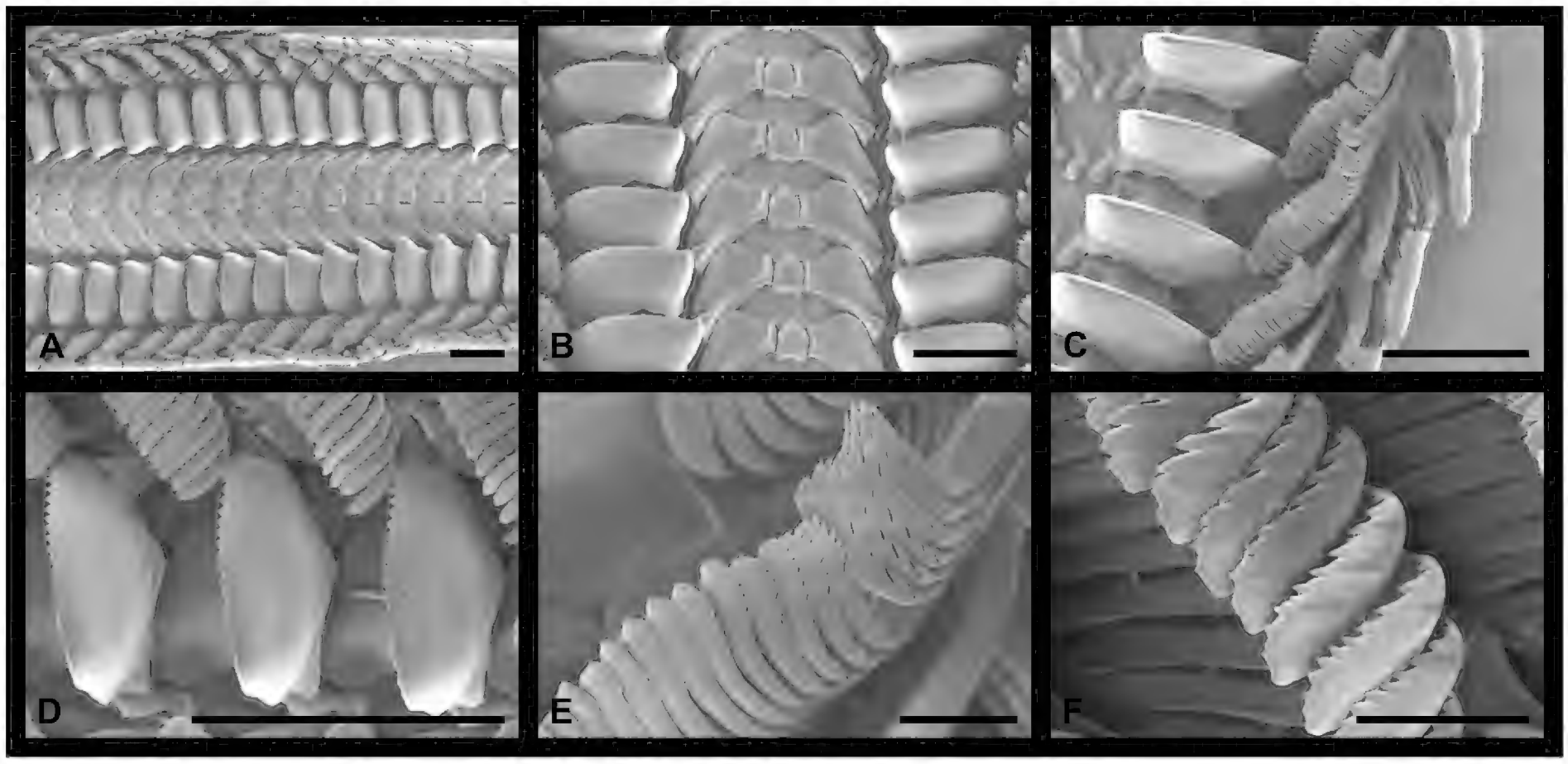

Figure 28. Radula of *Theodoxus wilkei* Sands & Glöer sp. nov. paratypes (UGSB 20687). **A**. Portion of the radula showing full sets of teeth; **B**. Magnified view of the central and lateral teeth; **C**. Magnified view of the lateral and first and second rows of marginal teeth; **D**. Magnified view of the lateral teeth; **E**. The first row of marginal teeth; **F**. Magnified view of the faces of inner marginal teeth belonging to the first row. Scale bars: 100 μm (A–D), 20 μm (E–F).

attenuated ridge, broader at cusp. B-central diminished, forms irregular "S" shape. C-central equally diminished, partly hidden below lower edge of E-lateral. E-lateral is simple, semi-smooth to serrate on upper edge. First layer of marginal teeth comprises 37–40 teeth, which decrease in size away from E-lateral but increase in size and bear serrations on edges of small faces; semidetached from second layer, which is fused and forms outer wall.

Differentiating features. The hemispherical, glossy black, black with white speckles or pure ivory, and finely striated shells of *T. wilkei* sp. nov. are easily differentiable from *T. altenai*, which displays light ivory checks on a dark brown-black background (Figs 4A–G, 27A–J), and *T. gloeri*, which lacks shell pigmentation and bears strong axial ribs on the shell (Figs 11A–C, 27A–J). However, using only conchological features of periostracum colouration and patterning and shell shape, it is still challenging to differentiate *T. wilkei* sp. nov. from some morphotypes of *T. anatolicus*, *T. baeticus*, *T. fluviatilis*, *T. gurur* sp. nov., *T. jordani*, *T. macri*, *T. major*, *T. pallidus*, *T. syriacus*, *T. velox*, and *T. wesselinghi* sp. nov., which can share similar shell shapes and colouration patterning (Figs 5A–M, 6A–G, M, 7M–P, 8A–D, 10E–H, 13A–G, 15P–R, 16C–P, 17A–E, 18A–G, 19O, P, 20A–D, I, J, 21A–D, I–R, 22I, J, 24E–J, 27A–D). *Theodoxus wilkei* sp. nov. can be distinguished from Anatolian morphotypes of *T. baeticus*, which typically displays ivory blotches on brown background (Fig. 7A–D); *T. jordani*, which typically displays brown diagonal zig-zag line patterning on an ivory background (Fig. 15E–L); and *T. velox*, which has white-ivory stripes on a dark background (Fig. 22K–M). Finally, the bright yellow to deep orange calcareous base of the operculum in *T. wilkei* sp. nov. can help to distinguish it from *T. altenai*, *T. anatolicus*, *T. baeticus*, *T. jordani*, *T. macri*, *T. major*, *T. pallidus*, *T. syriacus*, and *T. wesselinghi* sp. nov., which typically have lighter calcareous bases ranging from ivory to cream (Figs 4–8, 13, 15–21, 24); *Theodoxus gurur* sp. nov., differs in having a light to dark brown operculum (Fig. 13, 27).

There are a number of structural differences on the operculum. The attenuated apophysis in *T. wilkei* sp. nov. allows a distinction from *T. altenai* and *T. jordani* (Figs 4, 15, 17, 27). The presence of a rib-shield and rib-pouch further discriminate *T. wilkei* sp. nov. from *T. altenai*, *T. anatolicus*, *T. jordani*, and *T. macri*, where these features are either absent or extremely diminished (Figs 4, 5, 15, 17, 18, 27). Furthermore, the rib-shield in *T. fluviatilis* and *T. baeticus* is typically broader than in *T. wilkei* sp. nov. (Figs 6–8, 9, 10, 27). Additionally, the lack of a pseudo-apophysis differentiates the new species from *T. altenai*, *T. anatolicus*, *T. baeticus*, *T. gurur* sp. nov., *T. jordani*, and *T. macri* (Figs 4–8, 13, 15–18, 27). Furthermore, the more rounded left adductor of the operculum base is only shared with *T. syriacus* and *T. wesselinghi* sp. nov. (Figs 21, 24, 27). The strongly defined callus on the top right edge of the operculum base in *T. wilkei* sp. nov. is only shared with *T. anatolicus*, *T. fluviatilis*, *T. major*, *T. pallidus*, and *T. wilkei* sp. nov. and may be used to differentiate this species from all others (Fig. 27D).

Concerning the radula, *T. wilkei* sp. nov. can be distinguished from *T. gurur* sp. nov. by a square to triangulate R-central face (Figs 14B, 28B). The serrations on the upper edge of the E-lateral distinguish this species from *T. wesselinghi* sp. nov., *T. fluviatilis*, and *T. gurur* sp. nov., which have smooth, blade-like edges (Figs 14B, C, 27C, 28B–D; also see Zettler 2008).

Remarks. *Theodoxus wilkei* sp. nov. forms a part of a larger clade that includes *T. syriacus* and *T. wesselinghi*

sp. nov., where it shares a closer sister-species relationship with *T. wesselinghi* sp. nov. (Sands et al. 2019a; Fig. 2). The three species likely diverged from one another within a short time around the Pliocene–Pleistocene transition (Fig. 2).

Distribution. Only known from the type locality (Figs 3D, 26A, B).

Ecology. *Theodoxus wilkei* sp. nov. appears endemic to a freshwater spring environment with clear water (Fig. 26A, B). This spring environment is characterised by macrophytes in the littoral zone and a floor of small and large stones, rocks and course-grained sand (Fig. 26A, B). *Theodoxus wilkei* sp. nov. is particularly numerous on larger stones and rocks and co-occurs with *Pseudamnicola* and *Melanopsis* (personal observation M.E.G.).

Discussion

Most of the species discussed in this paper, including the new species *T. gurur* sp. nov., *T. wesselinghi* sp. nov., and *T. wilkei* sp. nov., are based on both morphological characters and molecular genetics (molecular data is only lacking for *T. gloeri*). Differences in the operculum and radula may be the most useful morphological features to distinguish species, which has already been suggested by a number of recent studies focusing on *Theodoxus* (e.g. Glöer and Pešić 2015; Alba et al. 2016; Anistratenko et al. 2017; Glöer 2018). Regarding the operculum (Fig. 1b), the presence or absence of apophysis, rib-shield, and rib-pouch and the sizes thereof, as well as the prominence of the callus seem to be conserved intraspecifically but vary interspecifically. The radula is equally informative in this regard (Fig. 1c), particularly concerning the shape of the R-central, ridging on the A-central, and the smoothness of the upper edge of the D-lateral. However, the radula is known for only few *Theodoxus* spp. making it challenging to differentiate species based on this trait alone. In contrast, shell pattern, colouration, shape, and size seem to be weak tools for differentiation (Fig. 1a). Only in selected cases can they be used to distinguish species (e.g. *T. altenai* versus *T. anatolicus*). This phenotypic plasticity is not surprising given that several authors suggested these conchological characters may be linked to environmental parameters (Neumann 1959; Heller 1979; Rust 1997; Zettler et al. 2004; Mienis and Rittner 2017).

Including our three newly described species, our checklist contains 14 *Theodoxus* spp. Of these, *T. velox* and *T. baeticus* are new occurrences for Asia (since Sands et al. 2019a). We updated synonymy lists based on the latest genetic and morphological evidence. For example, *T. saulcyi* (Bourguignat, 1852), *T. subthermalis* Issel, 1865, *T. heldreichi* (Martens, 1879), *T. euxinus* (Clessin, 1886), and *T. danasteri* (Lindholm, 1908) are here synonymised with *T. fluviatilis* (Linnaeus, 1758), and *T. michonii* (Bourguignat, 1852), *T. niloticus* (Reeve, 1856), *T. euphraticus* (Mousson, 1874), *T. mesopotamicus* (Mousson, 1874), and *T. octagonus* Eichhorst 2016 are synonymised with *T. jordani* (G.B. Sowerby I, 1836). Other Asian Neritidae attributed at times to the genus *Theodoxus*, such as *Theodoxus bicolor* (Récluz, 1843), *Theodoxus corona* (Linnaeus, 1758), and *Theodoxus reticularis* (G.B. Sowerby I, 1836) from further east (Madhyastha et al. 2010; Tripathy and Mukhopadhayay 2015), have more recently been attributed to the genus *Clithon* Montfort, 1810 (Quintero-Galvis and Raquel Castro 2013; Fukumori and Kano 2014; MolluscaBase 2019). This placement is based on the species' preferences for more saline environments (Tripathy and Mukhopadhayay 2015), planktonic life stages (Fukumori and Kano 2014), and, where tested, molecular data (Quintero-Galvis and Raquel Castro 2013).

The occurrence data of the 14 Asian *Theodoxus* spp. suggest five are widespread throughout the Western Palearctic (*T. baeticus*, *T. fluviatilis*, *T. jordani*, *T. major*, and *T. velox*), while the remaining nine are restricted to the region (*T. altenai*, *T. anatolicus*, *T. gloeri*, *T. gurur* sp. nov., *T. macri*, *T. pallidus*, *T. syriacus*, *T. wesselinghi* sp. nov., and *T. wilkei* sp. nov.). Of the five widespread species that also occur elsewhere in the Western Palearctic, *T. fluviatilis*, *T. jordani*, and *T. major* appear to be common across large areas of western Asia, while *T. baeticus* and *T. velox* are more restricted (Fig. 3). *Theodoxus velox*, which is common in the northern drainages of the Black and Azov seas and extends up to the Baltic Sea, was only found in Lake Sapanca in the study region (Fig. 3C). *Theodoxus baeticus*, which is widespread across the Iberian Peninsula, the Balearic Islands, Sicily, Tunisia, and the Balkans, is in Asia restricted to drainage systems of the Gulf of Gökova in Turkey (Fig. 3A). Of the nine species found only in Asia, five appear to be endemic to small regions: *T. anatolicus* (south-west Anatolia; Fig. 3A), *T. macri* (Cilicia and south-east Anatolia; Fig. 3A), *T. pallidus* (southern Iran; Fig. 3B), *T. syriacus* (south-east Anatolia and north-west Mesopotamia; Fig. 3D), and *T. wesselinghi* sp. nov. (central Anatolia; Fig. 3D). Each of the other four species are endemic to smaller systems or even single locations: *T. altenai* (Antalya; Fig. 3A), *T. gloeri* (Balıkdamı Wetland; Fig. 3D), *T. gurur* sp. nov. (Subaşı spring; Fig. 3A), and *T. wilkei* sp. nov. (Çifteler spring; Fig. 3D).

The International Union for the Conservation of Nature (IUCN) currently only recognises seven of the 14 Asian *Theodoxus* detected in this study. Apart from the species described here as new, the following four have not been evaluated: *T. gloeri*, *T. macri*, *T. pallidus*, and *T. velox*. Moreover, two of the eight are marked as "Data Deficient", i.e. *T. pallasi* (= *T. major*) and *T. syriacus*. Of the remaining five species assessed, two remain "Least Concern" (*T. fluviatilis* and *T. jordani*), one is "Near Threatened" (*T. anatolicus*), and two are "Critically Endangered" (*T. altenai* and *T. baeticus*; note however that the latter species is in need of re-evaluation following the revisions presented by Glöer (2018), Sands et al. (2019a), and the present paper). Based on the data we present here, we formulate recommendations following IUCN guidelines (criteria A or B; IUCN Standards and Petitions

Committee 2019) for the conservation status assessments for the species without sufficient data available ("Data Deficient") or those not evaluated by the IUCN as yet:

Theodoxus gloeri. We consider this species "Critically Endangered" (CR). The species is only known from two sites in very close proximity at a single location. Odabaşı and Arslan (2015) suggested it maintains a subterranean lifestyle, as such the area of occupancy is unlikely to be larger than 10 km^2. Recently one of us (M.E.G.) visited the location but could not find this species and further noted the pumping of water for irrigation close to the location. This indicates a decreasing quality of the habitat. Moreover, no specimen of this species has ever been found alive.

Theodoxus gurur sp. nov. This species is only known from one small locality (Suyunbaşı spring). The distribution area as such does not exceed 1 km^2. The spring, which forms part of a recreational park, is subject to high human activity, and there is growing anthropogenic impact such as personal waste from frequenters (personal observation M.E.G.). Moreover, much of the original spring system has been pooled and channelled along man-made structures. The quality of the habitat is decreasing. The threats to this species are similar to that of *T. altenai*, which is marked "Critically Endangered" (CR), and we thus recommend classification as CR accordingly.

Theodoxus macri. This species is challenging to assign a conservation status given the taxonomic concerns (see above). If historical identifications are to be taken as accurate, this species has suffered from a serve reduction in the extent of its distribution range. However, the conservation status rises and falls with the accuracy of former identifications (e.g. those in Israel and Jordan). Nevertheless, this species can still be found over a distribution extent of at least 10,000 km^2 and likely occurs in >10 locations, across eastern Cilicia and parts of south-eastern Anatolia. It is therefore unlikely to be "Endangered" (EN) or "Vulnerable" (VU). We propose either "Near Threatened" (NT) or "Least Concern" (LC) depending on the above.

Theodoxus major. We propose this species to be classified as LC. While the species has incurred a reduction of range given regional extirpation in the Aral Sea (Andreev et al. 1992; Aladin et al. 1998; Micklin et al. 2014), it still occupies a very large distribution range and is common within the Caspian and Azov drainage basins. Moreover, it has expanded into man-made channels between the Volga and Don rivers (personal observation A.F.S.), which suggests it may be tolerant to some anthropogenic activities.

Theodoxus pallidus. Sands et al. (2019b) have demonstrated that this species is in a demographic decline, potentially linked to human and climatic influences on the environment. During sampling for this species, a number of spring systems in the region, from which this species has been reported in the past, had dried up, were no longer in existence, or the species could not be found (personal observation A.F.S.). Due to the loss of habitat it is estimated that a population size reduction of at least 30% has occurred over the last three decades, and it is suspected that continued climatic instability and increasing demand for water resources will likely drive further declines as suitable habitat diminishes. We suggest classifying this species as VU. Moreover, while this species can still be found in a number of isolated sites in southern Iran, the area of occupancy is unlikely to exceed 2,000 km^2, where the species' distribution is highly fragmented.

Theodoxus syriacus. This species occurs in a number of springs and streams over a large geographic extent between south-eastern Anatolia and Mesopotamia. However, the species has suffered from a serve reduction in its distribution range. The continued existence of this species in Lebanon and southern Syria for example are dubious (see distribution for this species above). Given the reduction of the geographic distribution, we suspect some decline in the population size. As such, we propose this species be treated as NT.

Theodoxus velox. Although the range of this species is restricted in Asia, it can be found in numerous locations across Eastern Europe, particularly in the drainages of the Black and Azov seas of Ukraine. Data from Sands et al. (2019a) show this species has a much wider distribution extent than originally attributed. We consider this species as LC.

Theodoxus wesselinghi sp. nov. This species is currently only known from four isolated locations in central Anatolia and the known distribution range does not exceed 10,000 km^2. Additionally, the spring locality in Fele, İsparta has gone through severe alteration. Regular usage by locals for water and its location adjacent to a major road also jeopardises the persistence of the species at this location. We consider this species VU.

Theodoxus wilkei sp. nov. Similar to *T. gloeri* and *T. gurur* sp. nov., this species has a small area of occupancy (<1 km^2) and only occurs at a single location (Çifteler spring). As part of a recreational park the spring is affected by high anthropogenic impact, especially as a direct consequence of recreational activities (e.g. swimming) and pollution (e.g. plastic litter) (personal observation M.E.G.). We thus propose this species to be treated as CR.

In summary, conservation efforts in Asia should focus on species with narrow distribution ranges, especially those under greater threat from climatic change and anthropogenic impact. Additionally, future research is required to assess conservation statuses of European and North African *Theodoxus* spp. not discussed herein. Six more species have been confirmed through molecular analyses for those regions: *T. danubialis* (Pfeiffer, 1828), *T. marteli* (Pallary, 1918), *T. numidicus* (Récluz, 1841), *T. subterrelictus* Schütt, 1963, *T. transversalis* (Pfeiffer, 1828), and a potentially new species from Caravaca, Spain (Sands et al. 2019a; Fig. 2). Recommendations from molecular studies (Bunje and Lindberg 2007; Sands et al. 2019a; Fig. 2), such as the suggested synonymy of *T. prevostianus* (Pfeiffer, 1828) and *T. danubialis*, still need to be officially implemented and updated. Moreover, the status of some morphospecies, such as *T. hispalensis* (Martens, 1879), *T. maresi* (Bourguignat, 1864), *T. peloponensis*, and *T. valentinus* are dubious given the variation

in operculum structure or similarity with other species (Kirstensen 1986; Martínez-Ortí et al. 2015; Sands et al. 2019a; Fig. 2). These morphospecies still require phylogenetic assessment in conjunction with a review of the type material to warrant proper conservation consideration.

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Supplementary material 1

Supplementaty tables

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Data type: species data

Explanation note: **Table S1.** Collection, location and GenBank accession details of all specimens incorporated into the phylogeny. **Table S2.** Collection details of all specimens and type material photographed for the current study. **Table S3.** Divergence dates and highest posterior densities of nodes labelled in the phylogeny (Fig. 2).

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